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INTERRELATIONSHIPS OF THE SPOROZOA.

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OTHER things being equal, it is perhaps an easier task to determine the interrelationships of a group of parasites than those of a series of free-living forms. Once the parasitic habit is acquired, development is confined within narrow limits. Two definite lines are followed. These are: morphological degradation, and complication of the life history combined with increased fecundity. It is perfectly evident why this should be. Individually, the parasite is at once relieved of two of the great problems of animal existence. These are: the obtaining of food and the avoidance of serving as food for some other animal. The parasite has no enemies and abundant food surrounds it on all sides. As a result, various parts necessary to a free-living animal are lost. These are: the organs concerned with the capture and digestion of food, and those which serve as protection against the attacks of enemies. On the other hand, the new mode of life involves new needs, and the organism responds by the production of new organs. Such are: hooks, providing for the maintenance of a fixed position, and, in many cases, beaks or rostra which enable their possessors to bore through the tissues of the host.

Finally, a parasite acquires the ability to resist being digested. This appears in some cases to result from the formation of a differentiated external layer, but in general it is to be credited to some property of the living protoplasm. It is, necessarily, a property possessed by all organisms which live within others, and hence has no taxonomic value.

But if the existence of the individual is rendered easier, that of the species is menaced by a danger not experienced by free-living forms. With these, birth, growth, and reproduction all take place in free nature. For the most part, the eggs and young are left to shift for themselves, but the dangers which they encounter, are much the same as those which threaten the adults. The greater mortality during these stages is primarily due to their greater helplessness. But it is far different in the case of parasites. For these the course must, so to speak, consist of a series of leaps. A given host, at best, eventually dies and its death involves that of its parasites, as individuals. Hence the eggs or spores must be transferred to another host or else the species will cease to exist. Parasites are so abundant, and so thoroughly well established that we are prone to overlook what a radical departure this is from the ordinary scheme of animal life. The elements destined to tide the species over this critical period reach the exterior in one of several ways. The more usual are either by the death of the host, or by being carried out with its fæces. Ordinarily animals do not eat either their own dead or their own fæces, whence the only chance the germ has is to become attached to the food and so swallowed. Accordingly, as a general rule, parasites are common in social and uncommon in solitary animals. The termites, which do eat their fæces, invariably have their intestines literally packed with the curious Trichonymphidæ.

The response of the species to this acquired peril is two-fold. Complications are introduced into the life history. These are of such a character as to increase the probability of obtaining lodgment within the appropriate host. This is the most striking feature displayed by parasites. The other response is the acquisition of great fecundity. Great stress is always laid upon this, yet it is after all doubtful if parasites, taken as a whole, do

actually exceed other less specialized forms of life in their reproductive powers. Nevertheless the germs are produced in such numbers that if one in many thousands survive, the perpetuation of the line is assured.

Examples in support of the statements given above are numerous. Certain animals, particularly the small Nematodes, live indifferently either in the outside world or else upon or within higher forms. Such may be regarded as upon the threshold of the parasitic life. A second step is taken by those Flagellates which inhabit the recta of frogs and salamanders. These animals are morphologically like their free-living congeners nor is their life history known to be more complicated. But turning to the flat-worms we find the parasitic habit in its most confirmed aspect. This phylum, moreover, furnishes us with a series of stages from typical free-living forms to typical parasites. It is divided into three classes: the Turbellaria, the Trematoda, and the Cestoda. The first class consists mainly of free-living animals, and is characterized by an alimentary canal and a ciliated epidermis. The Trematoda retain the intestine, but have lost the cilia. The Cestodes go farther, and losing all trace of an alimentary canal, absorb their nutriment through the epidermis. There is thus a progressive morphological degradation.

But along with this change in the individual, there is a striking change in the life history. In the free-living Turbellaria and the ectoparasitic Trematodes, development is direct. That is, the eggs produce young which grow to be adults without metamorphosis. On the other hand, the endoparasitic Trematodes and the Cestodes bear off the palm for a complicated life history. The organisms hatched from the eggs are wholly unlike the adults, and there is always at least one metamorphosis. In addition, change of host is invariable. Thus, the liver fluke of the sheep spends a part of its existence in a water snail. Indeed, from a purely utilitarian standpoint, these animals appear to have overshot the mark, and their ontogenetic development defies a rational explanation. The desired end could apparently have been reached quite as certainly by less devious methods. But while we cannot explain the *raison d'être* for such processes, it is evident that they indicate a confirmed parasitism. These

animals are without doubt the descendants of a long line of parasitic ancestors and they probably represent the limit to which the habit can go.

We are thus furnished with two criteria enabling us to gauge the modifications induced by this mode of life. That is, given two allied groups of parasites, that possessing the more degraded organization and more complex life history is to be considered as the less primitive. A third criterion is furnished by the part of the host chosen for a habitat. Without doubt, the original gateway was the mouth or the rectum. Thus the less modified parasites are inhabitants of the alimentary canal. Examples are such animals as *Amœba blattæ* and the various Flagellates mentioned above, which dwell in the recta of frogs and salamanders. Access to the lungs and liver is also easy, although some of the parasites of the latter organ reach their chosen place by an indirect path. In the case of the inhabitants of the sexual organs, muscles, and brain, the infection comes in most cases by way of the intestine. There is, however, no direct road and the parasite must bore its way through the tissues of the host. These parasites are generally of the most modified types. On the contrary, the greatly modified Cestodes, at least in one of their hosts, live in the alimentary canal. This criterion, then, needs to be used with much more caution than the other two.

Having obtained certain criteria, I shall endeavor to apply them to the matter in hand, as indicated by the title of my communication. The Sporozoa stand alone. Their ancestors were in all probability Protozoan, but they branched off at so early a period that there remain absolutely no connecting links between them and any of the other classes of the Protozoa. There are two rival views regarding their origin. Minchin [1] aptly terms these the euglenoid and the amœboid hypotheses. The one regards the Flagellates, the latter the Rhizopods, as the ancestral forms. Bütschli has advocated the former, whereas Minchin pronounces in favor of the latter. To me, however, it appears that neither can be adopted without reserve. Each, by implication, assumes that all Sporozoa have had a common

[1] *A Treatise on Zoölogy*, edited by E. Ray Lankester, Chapter I, Section K.

origin, which, for reasons that I shall give, does not appear to be the case.

The class itself falls readily into two subclasses: the Telosporidia and the Neosporidia. In the former, arrived at a certain stage of its existence, the individual divides into reproductive elements, the spores, and ceases to exist as an individual. In the latter, vegetative growth and spore formation proceed hand in hand. Further, the Telosporidia display sexual differentiation of fully as definite a character as the mammals, while nothing of the sort has as yet been described for the Neosporidia.

The division into lesser groups is as follows: —

TELOSPORIDIA.

Order 1, *Gregarinida.*
  Suborder 1, Schizogregarinæ.
  Suborder 2, Eugregarinæ.
    Tribe 1, Acephalina [Monocystidea].
    Tribe 2, Cephalina [Polycystidea].
Order 2, *Coccidia.*
Order 3, *Hæmosporidia.*
  Suborder 1, Hæmosporea.
  Suborder 2, Acystosporea.

NEOSPORIDIA.

Order 1, *Myxosporidia.*
  Suborder 1, Phænocystes.
  Suborder 2, Cryptocystes.
Order 2, *Sarcosporidia.*
Order 3, *Haplosporidia.*

This is Minchin's classification, excepting the fact that I have included the Haplosporidia. Doflein [1] rates the Coccidia and Hæmosporidia as suborders, the two making up the order Coccidiomorpha. This is probably an improvement.

[1] *Archiv für Protistenkunde*, vol. 1, 1902.

Of all the Telosporidia, the Polycystidea stand highest in organization. Their name indicates the fact that they are divided into parts. The division is longitudinal and the parts, from before backward, are termed epimerite, protomerite, and deutomerite. The epimerite is an organ of attachment, comparable to the suckers of Trematodes and the hooks of Cestodes. It is peculiar to the Polycystidea and has evidently been evolved to meet the requirements of an intestinal life. The protomerite and deutomerite are the two "cysts" of the gregarine body. The latter is nearly always much the larger, and contains the nucleus.

From without inward, the ectosarc of a Polycystid gregarine shows epicyte, sarcocyte, and myocyte. The epicyte is a membrane of some formed substance. Its function is probably to guard against the too rapid action of the fluids of the host's intestine. The sarcocyte in protoplasmic and an ingrowth from it forms the septum which separates the protomerite from the deutomerite. The myocyte is a muscular system of longitudinal and transverse fibers. By means of various contractions of these fibers gregarines are able to change shape and to display locomotor movements.

It is thus seen that as regards both form and anatomy the Polycystids are somewhat complicated animals. They are also exclusively intestinal parasites and there is neither change of hosts nor alternation of generations. If then our criteria be of any value, the Polycystid gregarines are the least modified of the Telosporidia and stand nearest to the stem from which the entire subclass originated. Assuming this as a working hypothesis, it remains to be seen if the remainder of the Telosporidia can be derived from them.

Gregarines develop from a minute protoplasmic body, known as a sporozoite. The sporozoite is piriform or vermiform. At the anterior end, the protoplasm is stiffened and forms the so called rostrum, by means of which the organism is able to work its way into an epithelial cell of the host's intestine. As a rule, penetration is only partial and the Polycystidea, with the exception of a single family (the Stenophoridæ), are never cell parasites. In its chosen place, the sporozoite grows to be an adult

gregarine, or trophozoite. In most cases, the attachment to the host epithelium is sooner or later lost and the gregarine takes up a free life in the intestine of its host. In some species the attachment is maintained until the animals are sexually mature, but the distinction is not important.

Although lacking in secondary sexual characters, the adult gregarines are male and female. We owe this knowledge to the recent brilliant work of Léger. At the proper period, two of opposite sex come together, conjugate, and form a cyst. Within the cyst, the male gregarine produces motile, tailed elements, the spermatozoids. The female gregarine produces rounded cells, the eggs. At maturity, the spermatozoids seek and fertilize the eggs. Each fertilized egg eventually produces a spore, the contents of which septate into eight sporozoites. Ordinarily, the cysts reach the exterior shortly after their formation, and sporulation takes place while the cyst is lying on the earth. It may, however, be completed with the cyst still in the host intestine, but auto-infection has never been described.

Eventually the cyst opens and the spores are set free. These, if they reach the intestine of another individual of the host species, dehisce and release the sporozoites. Otherwise their fate is doubtless death.

In the classification given above, the Gregarinida are ranked as an order. This order is divided into two suborders: the Schizogregarinæ and the Eugregarinæ. The former includes those animals originally termed the Amœbosporidia. They possess a fixed body form, but their anatomy is much simpler than that of the Eugregarinæ. There is an alternation of generations. So far, however, but four or five species are known, and this rarity appears to be actual and not merely the result of insufficient study. For the time being, it appears best to regard them merely as a small offshoot from the Eugregarinæ.

The Eugregarinæ are divided into tribes. In the more recent general works, these are named the Cephalina and the Acephalina. There does not seem, however, to be any good reason for abandoning the older terms Polycystidea and Monocystidea. Except for the interpolation of the Schizogregarines, this classification is the same as that which has been in vogue for many years.

Its implication is that the relationship between the Polycystidea and Monocystidea is very close. Relatively, this is true, yet there are considerable differences. For one thing, reproduction in the Monocystids is isogamous. The encysted trophozoites each break up into gametes, which are all alike. These gametes fuse in pairs to form the zygotes. It is assumed that in each zygote, one gamete has been derived from one trophozoite and the other from the other, but the point is necessarily almost impossible to demonstrate. Each zygote produces a spore.

In the second place, the Monocystidea are far simpler in organization than the Polycystidea. While some of them possess a definite body form, many do not. Moreover, as their name indicates, their bodies are never divided into two chambers, a result of the loss of the sarcocyte. It is on this same account, in all probability, that they are polymorphic. Now, throughout the Polycystidea a perfect series can be established based on the development of the sarcocyte. In some it is always thick and continuous all over the body. In others it is but feebly developed, while in a certain number the septum disappears, and these species simulate the Monocystidea. The element is obviously in a transitional state, and since we are dealing with parasites, we are warranted in supposing it is disappearing.

Considering next the life history, the Monocystids, like the Polycystids, develop from a sporozoite which is released in the intestine of the host. But whereas in the latter group the sporozoite never gets farther than the intestinal epithelium, in the former it penetrates the cœlome. Some Monocystids develop in the connective tissue surrounding the intestines of their hosts, whereas others go farther. Thus, in the Monocystids of the earthworm, the sporozoites gain the seminal vesicles before developing into gregarines.

We are thus furnished with certain data enabling us to determine which of these two groups is ancestral. The evidence awards this distinction to the Polycystidea. That furnished by the sarcocyte is very suggestive, and the Monocystidea, which lack it, are to be considered the derived group. The life history points in the same direction. It is to be assumed here, as it is in the case of most animals, that ontogeny recapitulates phy-

logeny. That is, the Monocystids have arisen from certain sporozoites, which have pushed their way entirely through the intestinal epithelium instead of remaining either attached to it or within it. Finding in this way a congenial environment, they have survived and eventually established a new group of animals.

It is thus possible to decide which of the two modes of reproduction displayed by these two groups is the more primitive. On *a priori* grounds, heterogamy can be derived from isogamy or isogamy from heterogamy. But, presumably, the more primitive group will display the more primitive mode of reproduction. Whence the conclusion appears justifiable that the lack of sexual differentiation in the Monocystidea is the result of a loss. This conclusion is supported by the fact that, in the other Telosporidia, the organisms are male and female.

The life history of a Coccidian begins in precisely the same way as that of a gregarine. A sporozoite, released in the lumen of the intestine, seeks and penetrates an epithelium cell. From this point, one of two courses may be followed. Easily satisfied, the sporozoite may settle down at once within the cell it has entered, and proceed to grow. Or else it may completely pass through the intestinal wall, and eventually come to rest within a cell of the liver, kidney, or testis. In either case, once established, the organism grows until it reaches a certain definitive size. Then, by a process termed schizogony, it divides into a number of merozoites. These seek fresh cells, which they invade. The schizogonous cycle, which may be repeated many times, occasionally produces the parasites in such numbers that the host is killed. But whether or not, at the end of a certain time, the merozoites develop into male and female cells. Each male cell produces a number of minute elements, the microgametes. Each female cell develops into a single egg, or macrogamete. At maturity, the mobile microgametes seek and fertilize the eggs. Immediately after fertilization, the egg lays down a protective covering and becomes an oöcyst.

The process differs from that in the Polycystidea in two respects. In these, the female trophozoite produces numerous eggs and fertilization takes place within the cyst. In the Coccidia, each female trophozoite metamorphoses into a single egg,

and encystment follows fertilization. The attempts to homologize these two methods are not wholly satisfactory, and do not shed much light on the relationship of the two groups. It may be observed, however, that wherein the Coccidia differ from the gregarines, they approach the conditions found in the highest animals.

Accordingly, in the attempt to derive the Coccidia from the gregarines, it is advisable to seek evidence other than that furnished by the reproductive processes. This is furnished by the life history and the habitat. The Coccidia display an alternation of generations and live within cells. These are both indicative of a greater specialization than is shown by the gregarines. We may imagine that in evolution certain sporozoites penetrated completely within the cells of the intestinal epithelium, and there remained and developed. Such a habit, once acquired, would speedily lead to morphological degradation. The Polycystidea may almost be said to lead a free life. They possess and exert the power to move from place to place. But the Coccidia, living within cells, add to the degradation which follows from a parasitic, that which results from a sedentary habit. Two influences are thus at work upon them, and they have become the most simply organized of all the Sporozoa. Their form is spherical or ellipsoidal, that taken by any non-living liquid when in a state of equilibrium. Anatomically, they are merely nucleated masses of cytoplasm, not even displaying differentiation into ectosarc and endosarc.

It then seems justifiable to derive the Coccidia from the Polycystidia, although perhaps indirectly, for reasons which I shall give. The fact that some inhabit the internal organs of the host presents no difficulty. In numbers, those infesting the intestinal epithelium are much in excess. These were doubtless first evolved. The intracellular habit once acquired, the organ-infesting Coccidia could easily have arisen from those living in the intestinal epithelium. The more venturesome sporozoites, by passing entirely through the intestinal wall, finally gained one of the internal organs. The pabulum furnished by a kidney or testis cell being satisfactory, the line was established.

The last group of the Telosporidia is the Hæmosporidia.

This order is, in some respects, the best studied of all the Sporozoa, since it numbers amongst its members the parasites of malaria and yellow fever. In the acquisition of two hosts, it reaches a higher degree of specialization than the Coccidia, and extreme specialization is also indicated by the relative paucity in species. It is to be remembered, however, that from the biological side, the group is not so well known as either the Coccidia or the Gregarinida. Accordingly, generalizations valid to-day may need to be modified as our knowledge increases.

Two suborders have been established, the Hæmosporea and the Acystosporea. With the exception of one important feature, the life history of these two is the same. It is further essentially the same as that of the Coccidia.

As in the rest of the Telosporidia, the Hæmosporidian begins its career as a sporozoite. Set free in the blood of the host, this sporozoite attacks and enters a blood cell, preferably an erythrocyte. Here it grows into a trophozoite, which is amœboid in the Acystosporea and generally vermiform in the Hæmosporea. The trophozoite, growing at the expense of the blood cell, soon breaks up into a number of merozoites. By the disintegration of the blood cell, the merozoites fall into the blood stream. Forthwith they attack new blood cells and the process (schizogony) is repeated. The increase is therefore by geometrical ratio and as Minchin says: "It is evident that reproduction at this rate could only continue indefinitely in the *ichor* of an infinite host." Accordingly, at the end of a certain number of generations, the parasite provides for its future by the production of male and female elements.

So far the process is exactly parallel to that found in the Coccidia. In the Hæmosporidia, however, or rather in the Acystosporea, the male and female cells must be removed from the blood of the host to insure further development. This removal is effected by a blood-sucking insect (a mosquito) which takes the parasites into its alimentary canal. Here they mature, the male cells forming each a number of microgametes, the female cells each a single macrogamete or egg. The microgametes fertilize the macrogametes, which then metamorphose into elongated elements, the oökinetes. The oökinete pierces the

intestinal epithelium of the mosquito and comes to rest in the peri-intestinal tissue. There is first a period of growth, during which the element assumes a spherical form and becomes inclosed by a delicate wall. No actual cyst is developed. Eventually, the sporozoites are produced directly from the protoplasmic mass, the spore stage being omitted. Excepting for the fact that fertilization is postponed until after the removal of the parasite from the vertebrate host, that part of the Acystosporean life history which is passed in the mosquito corresponds exactly to that part of the Coccidian life history which is passed in the cyst.

The Acystosporea are parasitic in the blood of mammals and birds. Intermediate hosts are known in many cases, and they are generally assumed in the rest. The Hæmosporea, on the other hand, infest reptiles and batrachians. Intermediate hosts are not known,[1] nor can we readily believe that such forms are much preyed upon by Diptera. However greatly we may dread the mandibles of the mosquito, the Chelonia are probably indifferent to its attacks. Moreover, in the case of Lankesterella of the frog, it has been shown by Hintze [2] that sexual reproduction takes place in the blood, and that the motile zygotes so formed gain the epithelium of the intestine. Here they encyst, the cysts so formed eventually reaching the exterior by being carried out with the fæces of the host.

If the life history of Lankesterella may be taken as representative of that of the Hæmosporea, we find that the two suborders of the Hæmosporidia differ only in that the Acystosporea have acquired an intermediate host. While this is indicative of more extreme specialization, it is not difficult to imagine how it may have been brought about. The warm-blooded vertebrates have doubtless long been preyed upon by blood-sucking arthropods. The crucial point in the bringing about of this change of life on the part of the parasites was that some such blood-sucker would be unable to digest them. This would be merely a matter of chance. There was probably one time in their

[1] A case has, however, recently been described.

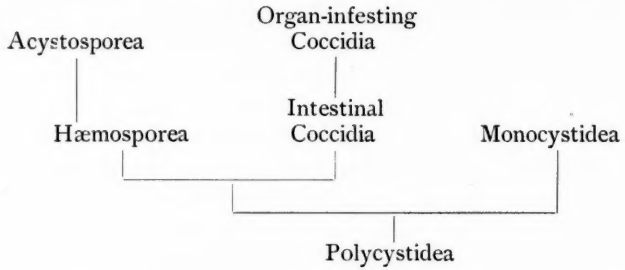
[2] *Zoöl. Jahrb., Abth. f. Anat.*, vol. 15, 1902, pt. 4, p. 693.

evolution when the Acystosporea could infect their vertebrate hosts in two ways, but the intestinal method is now lost. The acquisition of an intermediate host is obviously advantageous to the species, tending, as it does, to a wider distribution.

There are, however, anatomical differences between the Hæmosporea and the Acystosporea. The former, in the trophozoite stage, possess a definite body form, on which account they are often spoken of as Hæmogregarines. This definite form is due to the presence of a dense hyaline ectosarc, in which myocyte fibrillæ have been demonstrated. These animals, although typically cell parasites, indulge in frequent migrations in the blood plasma, and during such "free" phases, they display both contractile and locomotor movements. On the other hand, the trophozoites of the Acystosporea appear never to migrate. The blood cell originally attacked is abandoned only after the organism has divided by schizogony. No special anatomical differentiation appears to have been described, but the trophozoites undergo sluggish amœboid movements. Accordingly, as regards both the morphology and the life history, the Acystosporea are clearly the more specialized group. It next remains to relate the blood parasites with their closest relatives, the Coccidia.

As regards the life history, the parallelism is exact, except for the acquisition of an intermediate host in the Acystosporea. The sexual processes are practically identical. Morphologically, however, the Coccidia are practically on a par with the Acystosporea and considerably more degraded than the Hæmosporea. Comparing the Coccidia and the Hæmosporea, the former would, according to our criteria, be the derived group. But the favored habitat of the Coccidia is the epithelium of the intestine, and it seems as if this must have been occupied by Sporozoan parasites before invasion of the blood.

The view advanced by Minchin seems best to fit the case. This is that both Coccidia and Hæmosporidia have arisen from common ancestors. These ancestors in their turn I believe to have been derived from the Polycystidea, and my conception of the interrelationships of the Telosporidia is indicated by the following scheme: —



The habitat of the Polycystidea, the intestine of their hosts, has enabled them to lead a practically free life. Accordingly, they are the least modified of all Sporozoa, and have retained nearly as complex an organization as the Flagellates. They have given rise, on the one side, to the Monocystidea and on the other to the Coccidiomorpha. The former followed much the same lines as their immediate ancestors, but have undergone morphological degradation. The Coccidiomorpha became adapted to an intracellular life, and separated into two groups. In one of these, the inert Coccidia, morphological degradation has been carried to its extreme. The greater anatomical complexity of the Hæmosporea is to be credited to their habitat. The liquid blood offers a radically different environment from the motionless epithelium. In consequence, the power to move, possessed at the outset by the Hæmosporea as an inheritance from their Polycystid ancestors, has not been lost. Thus these animals possess the characteristic Telosporidian organ of movement, a myocyte. The Acystosporidia, further evolved, have apparently lost the ability to move from place to place. Their inertness, although comparable to that of the Coccidia, has been independently acquired. Finally, in their ability to display amœboid movements, they have not sunk quite so low.

Mesnil[1] considers the ancestral Telosporidian to be a Monocystid intestinal gregarine. Minchin derives the group from a hypothetical intracellular form. In both cases this ancestor is supposed to have given rise to existing gregarines on the one hand, and to the Coccidiomorpha on the other. To my mind,

[1] *Vol. Jubil. Soc. de Biol.*, Paris, 1899.

these hypotheses are open to objection in that they are based almost exclusively on the reproductive phenomena. They both involve the evolution of a more from a less complexly organized parasite. I have endeavored to show that this is contrary to what experience teaches us to expect. In our classification of the Metazoa morphology is given first place and it should not be neglected in a consideration of the Protozoa. The remarkable character of the reproductive phenomena displayed by the Sporozoa has, I think, given them an undue importance. The form of the adult animals has, in any attempt at a classification, at least equal value.

We have now to consider the Neosporidia. This subclass is but poorly known. As shown above, it consists of three orders, the Myxosporidia, the Sarcosporidia, and the Haplosporidia. The Myxosporidia are characterized by their peculiar spores, which bear a close resemblance to the stinging cells of cœlenterates. The spore consists of a bivalved shell, inclosing the sporoplasm and the polar capsules. The polar capsules, of which there may be from one to four, are tightly coiled filaments which occupy vacuities in the spore substance. Acted upon by the digestive juices of the host, the spore shell opens and the filaments are everted. By means of these filaments the spore is held attached to the intestinal epithelium of the host, and the sporoplasm escapes as a minute amœbula. Freed on the surface of a host cell, it works its way within and comes to rest. The nucleus presently divides, then the cytoplasm, and each spore thus produces a number of bodies which are at least the analogues of the Coccidian merozoites. They scatter throughout the host and each gives origin to a trophozoite. The trophozoite grows larger, becomes multinucleate and soon begins to form spores. These, eventually reaching the exterior, are fitted to infect new hosts.

The above outline of the life history is that given by Doflein. It is to be observed that there is no sexual process. Doflein, however, considers it possible that either the spores themselves may conjugate very shortly after their escape from the spore shell, or else that this process may take place between the young trophozoites. This he advances merely as a surmise, there being no observational evidence.

The young trophozoite may follow one of several lines of development. These lines diverge considerably. The nature of the forms so produced is indicated in the following table, which is taken from Doflein : —

Group I. Free-living forms.
Group II. Sedentary forms.
1. Inclosed in cysts.
2. In the state of "diffuse infiltration."
3. Cell parasites.

Group I contains the most highly organized of the Myxosporidia. Its members lead a free life in the gall bladder, urinary bladder, or kidney tubules of their hosts. They display differentiation into ectosarc and endosarc. The latter is essentially like that of other Sporozoa. The former is a clear granular layer. It is the seat of motion and gives origin to the pseudopodia. A myocyte does not appear to have been described. Throughout these animals resemble the Rhizopoda.

Group II is doubtless an offshoot from Group I, with the exception of the cell parasites. The encysted forms are those which come to rest at some point within the host's body. The part thus attacked reacts by the formation of a wall around the parasite, which is thereupon prevented from extending its explorations. "Diffuse infiltration" results when the parasite spreads out through a considerable region of the host's tissues. In such cases no cyst is formed. Eventually, these two kinds of trophozoites die as trophozoites, but leave the tissues which they had occupied, filled with spores.

The forms hitherto considered are mostly animals of considerable size, while the cell parasites, which belong to the suborder Cryptocystes, are amongst the smallest of the Sporozoa. The mode of life is, however, much the same. It is to this group that belongs the destructive *Nosema* (*Glugea*) *bombycis*, the cause of the silk-worm disease.

In no Myxosporidian is an intermediate host known, and infection is apparently always the result of chance. In those forms which live in such places as the gall or urinary bladder, the

spores are assumed to reach the exterior with the evacuations of the host. For the tissue-infesting species, however, there are no natural channels. Where the parts attached are superficial, it is conceivable that the tumors which so frequently occur in Myxosporidian infection may break to the exterior. In this way the spores would be set free. But in deep-seated infections the conclusion seems inevitable that the death of the host is necessary. This conclusion is supported by the fact that extensive infections are generally fatal.

The Myxosporidia attack cold-blooded vertebrates and arthropods. The Sarcosporidia confine their attentions to birds and mammals. They are very abundant in the visceral muscles of sheep and swine. While their spores differ from those of the Myxosporidia, the animals themselves are morphologically a good deal like those members of the last-named group which live in cysts or in the state of diffuse infiltration. Additional data regarding them are a crying need and at present all that can be said is that they have probably evolved from Myxosporidian-like ancestors. The Haplosporidia may be dismissed at once. Our knowledge is too scanty to warrant any generalizations.

It is possible, however, to compare the Neosporidia with the Telosporidia. Taking the free-living Myxosporidia on the one hand, and the Polycystidea on the other, we fail to detect any points of similarity. The habitats, life histories, and reproductive processes are wholly different. There is no morphological likeness in any of the stages, from spore to trophozoite. In a few cases, gregarines are almost amœboid and can protrude pseudopodia. The Monocystids, also, are cœlomic parasites and some species live in the organic cavities of their hosts. But this appears to be the sum total of the evidence indicative of any connection between the two groups. It is palpably insufficient.

Unless, then, future discoveries of a fundamental nature shall be made, there seems ample warrant for the view expressed by Mesnil and Doflein. This is that the Telosporidia and Neosporidia are not genetically connected. Accordingly, at least for the present, we should use the term Sporozoa merely as a convenient cloak. It serves to cover certain Protozoa which cannot be placed in any of the other Protozoan classes. It is not so long

since the so called Vermes subserved a like function among the invertebrates. Happily, in this case, confusion has been reduced to order and we who are interested in the Protozoa may hope that history will repeat itself.

WYNCOTE, PA.

CONTRIBUTION TO OUR KNOWLEDGE OF THE MYXINOIDS.[1]

JULIA WORTHINGTON.

Introduction.

Ever since Johannes Müller introduced the Myxinoids to the scientific world, interest in these primitive forms has continued unabated, both as regards their peculiarities of structure and function and their consequent position in the vertebrate series, and the interrelations of the different varieties among themselves. Owing to the wide geographical distribution of the Myxinoids, the relative scarcity of individuals, and the difficulty of securing material for study, especially the living animals, previous papers have been based upon the study of museum specimens, and our knowledge has, in consequence, been very incomplete. It was my good fortune to obtain, during the summer of 1904, several hundred individuals of *Bdellostoma dombeyi* Lac. in sound, healthy condition, which I kept alive in aquaria. I was able to provide conditions closely approximating their usual habitat, and, under these favorable circumstances, I kept them under constant observation for four months. The observations made have been checked by a study of the conditions of their normal habitat. This paper, therefore, is based mainly upon a study of living individuals in conditions approaching as nearly as possible the normal environment; and these notes are published in the hope of throwing some new light upon this interesting form, and for the purpose of correcting some erroneous statements that, through lack of means of observation, have gained currency.

I wish to express my thanks to Dr. C. H. Gilbert, of Stanford University, who kindly placed at my disposal the facilities of Stanford's seaside laboratory at Pacific Grove, California; to

[1] Under the direction of Dr. Howard Ayers.

Dr. Frank McFarland for helpful suggestions; and to Mr. M. H. Spaulding for much practical help. I wish also to thank Dr. Michael Guyer, of the University of Cincinnati, for the loan of laboratory materials, and to express my obligations to my sister Louise for the very excellent and accurate drawings from which the illustrations for Fig. 1 and 2 were made.

The Myxinoid upon which the following observations were made, is the common hagfish of the Pacific coast, *Bdellostoma dombeyi* Lac. It is found in exceeding abundance in the Bay of Monterey, where it is a great pest to the fishermen. It is caught both with hook and line, and in traps. Those caught on hooks do not live long in captivity. Instead of being hooked in the jaw as is usual with other fish, Bdellostoma usually swallows the baited hook whole, and is thus hooked through the head or the body wall, hence the esophagus and stomach are more or less torn in extracting the hook. Even under most favorable conditions I have not found those caught on hooks to live more than a few hours in aquaria. The traps used by the fishermen in catching hagfish, are large wicker baskets, loosely woven, resembling lobster pots. A quantity of bait, usually pieces of squid or sardines, is put inside, and the trap sunk over night. In the morning it may contain anywhere from twenty-five to a hundred fish, mostly medium size, with a few small and several large individuals. The largest hagfish are not caught in the traps, as the meshes of the baskets used are too small for them to pass through.

The aquarium, in which I kept them, was a wooden tank, about six feet long, four feet wide, and two feet deep. It was located in the basement of the laboratory, a large, cool room, well lighted. The water in the tank was kept about a foot deep, the bottom was covered with a thin layer of clean sand, and stones were loosely piled in one corner to furnish hiding places. Four streams of fresh salt-water, coming from glass pipettes, with a length of stream varying from two to four feet between the glass and the surface of the water, played constantly into the tank, supplying fresh, well aërated water. Here the colony lived throughout the summer. Although some two hundred and fifty fish were thus kept under observation,

not more than six or eight of the total number died a natural death. Of these two hundred and fifty, about seventy-five were kept in the aquarium from six weeks to two months or more before I killed them, and more than a hundred were kept for a month before being killed.

General Description.

It is not necessary to describe the general appearance or characteristics of Bdellostoma, as that has already been admirably done (Ayers, '94); but one or two points of interest were ascertained in reference to their size. Of 550 specimens measured, the longest was 24.5 inches, while 104 measured 20 inches or over, and 64 were between 19 and 20 inches long. When it is remembered that of these 550 specimens, between 350 and 400 were caught in traps that did not favor the ingress of the larger hagfish, the average length will be seen to fall in the neighborhood of 19 to 20 inches. In regard to their length at hatching, the smallest free-swimming hagfish that fell into my hands measured scant two and three eighths inches (60 mm.), while a few days later I took an embryo from the shell that measured a trifle more than two inches and a half (65 mm.). This embryo was apparently ready to hatch, as it swam vigorously as soon as it was freed from the shell.

These newly hatched hagfish have the same shape as the adult, the only perceptible difference between them and their elders being that their tentacles are relatively a little longer than those of the mature fish. At the time of hatching, the head is an eighth of an inch in diameter; when from twelve to fourteen inches long the proportions of head to body are somewhat different, the head measuring from three eighths to one half inch across, and thus being relatively thinner. When about fifteen inches long, however, the hagfish begin to increase rapidly in girth, measuring at least three fourths of an inch across the head, while the larger ones measure still more. This marked change of form does not, however, as might be thought, mark the time of sexual maturity, for an individual only twelve inches long and slim in proportion was found to have a well

developed ovary, with eggs in the process of yolk development. In regard to the age at which these changes take place, we have as yet no definite information. As is already known, the process of development within the egg is slow, when compared with the rate of growth of other vertebrate embryos; and their post-embryonic growth is probably also very slow, for very small fish (*viz.*, thirteen or fourteen inches long) kept in the aquarium for three months, showed at the end of that time no perceptible change in form or size, although they fed in a normal way, or at least, as normally as any other fish in the aquarium.

One of the most interesting points about Bdellostoma, because of its supposed taxonomic value, is the variation in the number of gills. Taking the number found in the hagfish of different geographic regions as a basis, the Bdellostomids have been divided not only into different species, but also into different genera, *Bdellostoma forsteri*, of the Cape of Good Hope, with its six to seven gills on each side being placed in one genus, and the Bdellostomas of the American Pacific coast in another, subdivided into two species, *Bdellostoma dombeyi*, with ten gill slits, found in Chilean waters, and *Bdellostoma stouti*, whose usual number of gill slits is eleven or twelve, in the waters of California. Dr. Ayers ('94), after a careful comparison of the Cape of Good Hope and California varieties, concluded that there was no specific, far less generic difference between the two forms, and stated that they, together with the Chilean variety, belonged to one species, the preferable name for which was *Bdellostoma dombeyi*. This conclusion was scouted by Howes ('94), but purely on *a priori* grounds, and without any study of the forms in question. Since this time not much work has been done that would throw light on this question until within the last year or two, when Dean, studying the hagfish found off the coast of Japan, came across a variety that he called *Homea okinoseana*, distinguished by having eight gills on each side, but in all other respects like the hagfish of other localities. This Japanese variety thus fills in the gap between the Cape form with its six to seven gills, and that of Chile, with ten gills on each side.

It is worth while to study the California form carefully and in detail with regard to the gills. Dr. C. H. Gilbert of Stanford

University, quoted by Jordan and Evermann states that in fifty-four specimens which he counted, forty-one had twelve gills on each side, twelve had eleven gills, and one had thirteen gills. He states also that he occasionally found one with ten or fourteen on each side, but that the normal number was twelve. Worked out in percentages, this would read : —

Individuals with 12 gills 75.9 %.
" " 11 " 22.2 %.
" " 13 " 1.8 %.

When tested by the examination of larger numbers of individuals, however, these figures undergo considerable modification, and a new factor enters in, *i. e.*, fish that have a different number of gill slits on the two sides. The following table is given by Dr. Ayers in his paper published in 1894 :—

101	individuals	had	11	gill	slits	on	both sides ;
26	"	"	11	"	"	"	one side and
			12	"	"	"	the other ;
208	"	"	12	"	"	"	both sides ;
11	"	"	12	"	"	"	one side and
			13	"	"	"	the other ;
8	"	"	13	"	"	"	both sides.
354	total number of individuals counted.						

Worked out in percentages this reads : —

Individuals	with	11	slits	on	each side	. . .	28.5 %
"	"	11	"	"	one " and		
		12	"	"	the other	. . .	7.3 %
"	"	12	"	"	each side	. . .	58.7 %
"	"	12	"	"	one " and		
		13	"	"	the other	. . .	3.1 %
"	"	13	"	"	each side	. . .	2.2 %

These figures, as will be seen, reduce the percentage of those having twelve slits on each side by one third, add very nearly one third to the percent of those with eleven slits on each side, increase slightly the percentage of those with thirteen on each side, and introduce the two intermediate forms, those with

eleven and twelve slits, and those with twelve and thirteen, these two together amounting to 10% of the total number. Dr. Ayers also says: "Of the eight 11–12 variation, where the position of the gills was noted, four had eleven gills on the right side, and twelve on the left, while the other four were just the reverse, with twelve gills on the right side and eleven on the left." On looking over the count of five hundred and fifty hagfish that I made while at Pacific Grove, I find still greater variability in the percents.

No. of Individuals	No. of Gills Left	Right	Percent
1	10	11	.18
3	11	10	.54
123	11	11	22.36
25	11	12	4.54
44	12	11	8.
325	12	12	59.09
7	12	13	1.27
15	13	12	2.72
7	13	13	1.27
550			

This larger count gives practically the same percentage of individuals with twelve gills on each side as do Dr. Ayers's figures, reduces that of those with eleven gills on each side about one fourth, increases the sum of the 11–12, and 12–13 variations from 10.4% to 16.5%, diminishes those having thirteen gills on each side from 2.2% to 1.27%, and introduces a new variation, 10–11 gills, this kind being .72% of the total number. This last variation makes direct connection with the Chilean variety with ten gills on either side. It will be noticed in my figures that in the three uneven variations, 10–11, 11–12, 12–13, the total number of individuals having the larger number of gills on the left side is sixty-two against thirty-three, almost two to one. This point will be discussed a little later.

The table following combines the records of Dr. Gilbert and Dr. Ayers with my own.

No. of Individuals	No. of Gills	Percent
4	10–11	.41
236	11	24.63
95	11–12	9.92
574	12	59.92
33	12–13	3.44
16	13	1.67
958		

A total of 958 individuals certainly gives a reasonably safe number on which to base conclusions. In this table as in the others, the fact stands out prominently that in the California hagfish twelve gills on each side is the number most commonly found. But when the number having it only amounts to 59.92% in a total of 958 eels, it cannot well be called the normal, or even the usual number, and consequently I agree with Dr. Ayers that the usual number of gill slits is eleven or twelve.

That 13.7% in a total of 958 eels is found where the number of gills is greater on one side than on the other, is to me one of the most significant features in the proper specific classification of the Bdellostomids. With six and seven gills the prevailing number in *Bdellostoma forsteri*, eight in that found in Japan, ten the number in the Chilean form, and eleven and twelve in California, varying on the one hand, though rarely, to ten, and on the other hand more frequently to thirteen, it is surely no longer possible to divide these animals into different genera and species on the basis of the number of gills alone; the count of teeth (Ayers, '94), is equally unsatisfactory as a ground for division into species, and no other ground for such division has ever been advanced.

As a matter of fact, the differing number of gills in the California hagfish is even more significant when the animal is examined more closely, externally and internally, than when the external apertures alone are counted. On dissecting the gill region of those animals with an unequal number of gills on the two sides, we find not merely that the number is variable, but also where the variation is most apt to occur. Referring back to my table, and noting the fish with an unequal number of gills

on the two sides, we find that the fish in which the greater number of gills lies on the left side (the side of the ductus œsophago-cutaneus), occur about twice as often as those in which the greater number is on the right side. But when the thoracic cavity of these particular fish was dissected, I found several cases where the number of external openings and the number of gills did not correspond.[1] Of the sixty-two individuals, in which the left gill slits outnumbered the right, six had the last gill on the left side, that which should open into the ductus, entirely wanting, making an even number of gills on each side. Two of these six were in the 11–12 group, four in the 12–13 group. In regard to the position of the external openings only one was at the normal distance from the ductus, in two the distance between ductus and external aperture was one half the normal distance between these openings, in two the external aperture lay very close to the edge of the ductus, and in one it lay in the cephalic edge of the ductus.

In other fish in which the number of gills on each side was uneven, where the greater number was on the left side, five had the last gill, that which opens into the ductus, rudimentary, varying from one fifth to one half the size of the normal gill, and in one of these the opening of the ductus was one half the usual distance from the external aperture nearest it.

In all of the fish examined by me that had the greater number of gills on the right side, the gills were normal, and normally placed. But another curious variant was found in the 12–11 series that has a marked bearing on the question, whether the change in the number of gills in the different varieties is due to addition or suppression. This individual had twelve gills on the left and eleven on the right side. The twelfth gill was of normal size and at a normal distance from its neighbor, but the second gill on the left side (counting from before backwards), was missing, the external opening leading into a short *cul de sac*. The first gill on the same side was rudimentary. If there were

[1] It should be stated here, that in counting gill slits, *i. e.*, the external apertures, the external opening of the ductus œsophago-cutaneus is always counted as one, as the external aperture of the last gill on that side usually lies not on the outer surface, but in the ductus just inside the opening.

either a fixed or a normal number of gills, this could only mean that this particular animal was a freak. But where we have variations of the species in which the number of gills ranges from thirteen to seven, and one variation (that from California), in which no number can be considered either normal or fixed, and where the last gill on one side is found to be either rudimentary or missing, there is certainly an indication of a tendency to the suppression of the gills. Moreover, in the last case the rudimentary and the missing gill are both in an unusual place (the cephalic instead of the caudal end of the line). Still another variant bears out this view. This variant was one of the even-numbered group, with twelve gills on each side. On opening the thoracic cavity, it was found that while the fish had twelve normal gills on the right side, on the left the first was missing, and the second rudimentary. As in the case last mentioned, the external aperture of the missing gill led into a *cul de sac* and there was no pharyngeal opening. In this fish there was no external mark to indicate the slightest abnormality within, which raises the question: What percentage of abnormality would be found if careful dissection were made of the gill regions of a large number of individuals?

There is no particular size in which these variations occur. In the last one given, the fish was only eleven and one half inches long; in the one preceding, twenty-one and one half inches long; the others varied between these two. It would be interesting if some young hagfish with an uneven number of gills, particularly individuals where the distance between the ductus and the nearest gill is less than normal, could be kept under observation for a number of years, to see if any changes occur during the life of the individual, or if these variations are fixed during larval growth and remain fixed during adult life. It would also be of great value in this connection if the other varieties of hagfish could be more carefully studied, to determine if the variation in the number of gills is as great as that of the California hag, and if so, when the variations occur. It should also be determined whether the number is more constant among the groups having a small number of gills.

HABITS AND HABITAT.

The hagfish abounds in the Bay of Monterey, and is taken on the regular fishing grounds, particularly on the rock-cod beds, at a depth of about three hundred feet. The bottom here is rocky and coated with a thin, smooth sediment, but without any great amount of sand or seaweed. Infrequently it is captured in shallower waters along shore where the bottom is sandy. From observation of several hundred individuals, I find that in the aquarium they evidently prefer the hard bottom when at rest, lying for the most part coiled in and out among the rocks, sometimes with their heads under cover, but more often with about two inches of the head projecting freely into the water. When not among the rocks, or not swimming, they rest coiled up on the bottom of the tank (Fig. 2), occasionally resting on the sand, but more often on the wood where the sand has been pushed aside. At a time when there were about thirty fish in the tank, I kept watch for a week to see how many chose the different kinds of bottom. I transcribe here the notes taken at the time.

July 24, A. M. All were among the rocks but two. Of these two, one was curled entirely on the wood, the other curled on the wood with its head resting on the sand.

July 24, P. M. Two were lying entirely on the wood, the rest were among the rocks.

July 25, Noon. The same as on the previous day. After pouring water on them vigorously, and so stirring them up to swim around, six settled finally on the wood, two of them with their heads resting on the sand, while the others returned to the rocks.

July 26, Noon. Two were on the wood, the rest among the rocks.

July 26, P. M. All were among the rocks.

July 27, A. M. Two were on the wood, the rest among the rocks.

July 28, Noon. One on the wood, the rest among the rocks.

July 29. Two on wood, one on sand, the rest among the rocks.

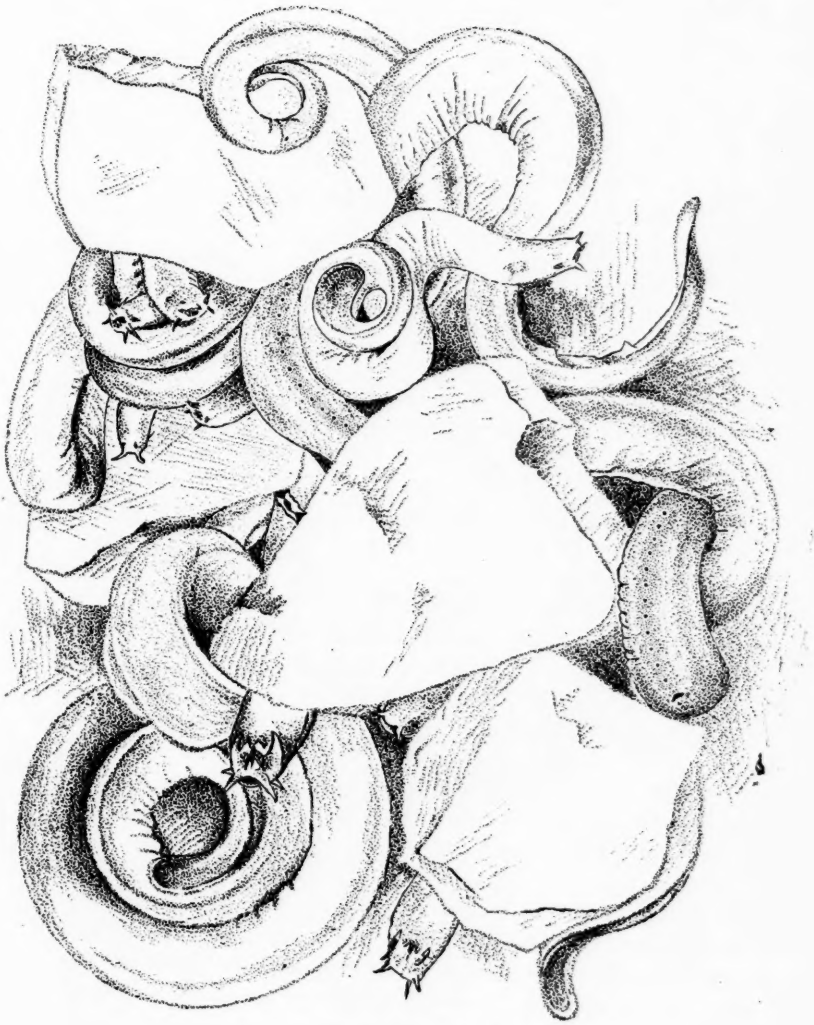


FIG. 1.—Hagfish coiled among the rocks. × ½.

July 30, A. M. Three on wood, one of them with its head touching the sand, the rest among the rocks.

July 30, P. M. Five on wood, the rest among the rocks.

Aug. 1, A. M. All among the rocks.

Aug. 1, Noon. Five on the wood, two of them partly touching sand, the rest among the rocks.

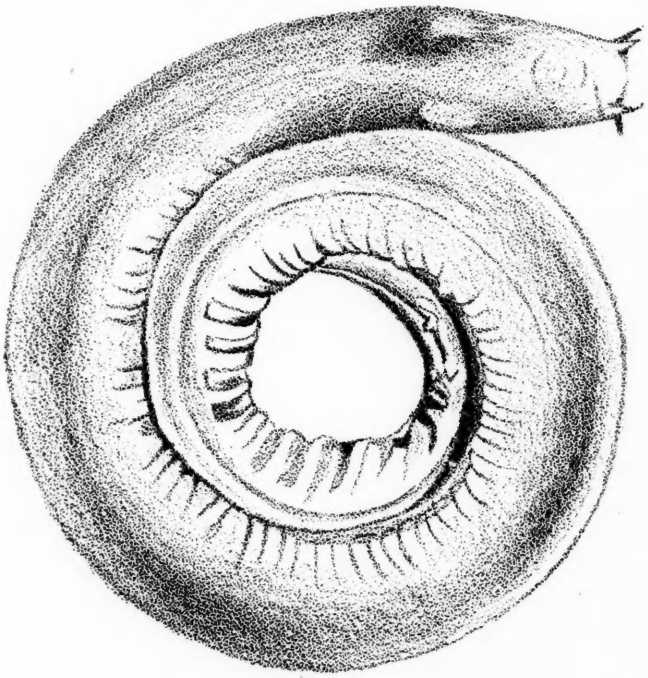


FIG. 2.— Hagfish at rest on the bottom of the aquarium. Natural size.

At a later date when there were one hundred and thirty fish in the tank, two more observations were made. The first showed only sixteen of the hundred and thirty fish on the sand, the second only fifteen. A few days later with one hundred and twenty-four fish in the tank, only twelve were on the sand.

Unquestionably then, in the ordinary circumstances of life, the hagfish prefers a hard bottom to rest on. If the rock heap

is overcrowded, and the bare wood spaces preëmpted, those left out will, for the most part, gather together and form a tangled coil, looking much like the conventional Medusa's head.

Perhaps another factor entered into this consideration of bottom, however. Was it altogether a feeling of touch that governed their choice of resting place, or did color play a part? Did they prefer the dark to the light? Two hagfish were transferred to an ordinary aquarium with glass sides and a zinc bottom. Half of this bottom was covered with sand to the same thickness as that in the large tank, and the sand and zinc were nearly the same color. The fish were kept here for several weeks, and acted just as they had in the large wooden tank. They coiled persistently on the hard zinc bottom, against the side of the aquarium, or against the iron waste pipe, seldom being found on the sand. After a few days I put a rock in the midst of the sand bottom, and after that one or the other would be found lying against it, but otherwise they shunned the sand, showing that it was purely a sense of touch that guided them.

The hagfish seem to have great power of resistance to unnatural environment, judging by the way they are handled by the Monterey fishermen, and the condition in which they reach the laboratory. They are taken from the traps between six and ten o'clock in the morning, dumped, fifty of them together, into an oblong can with a base about ten inches square and sides perhaps eighteen inches high, barely covered with water, and then stowed somewhere in the bottom of the boat while the fisherman finishes his business and rows to shore, a distance of two or three miles. Arrived on shore, they remain sometimes for several hours in the same uncovered cans before transportation to the laboratory. At the laboratory they undergo one more handling, as they are counted on being put into the aquarium. But in spite of this long wait in very little, poorly aërated water, but few die, though they are greatly crowded, and sometimes roughly handled. The long exposure to the air likewise seems not to affect them if the weather be not too warm, and the can not too full, so that the sun does not strike directly upon them. Of the first catch of about fifty, all lived; and of the second of one hundred and thirty-two, brought up in two

cans, thirty or forty were sick on arrival, but the next morning two only were dead, and all the rest in fine condition. It is noticeable that the young ones have, as a whole, more power of resistance than the old ones, for they would arrive fresh, as though just from the depths of the bay, no matter how sick many of the older ones were.

There is one unfailing test of the general condition of the hagfish: its geotropic reaction. When well and at rest, it is invariably coiled up more or less tightly, either in a spiral by itself (Fig. 2) or in and out among the rocks. Even if the fore part of its body lies free and sinuous, the tail is coiled. But if exhausted or sick, the coil straightens out, and it lies in a crescent form. The sicker it is, the straighter it becomes, and when dead it lies entirely straight.

The hagfish can live out of water without injury for a great many hours if kept in a cool, damp place. I often found on visiting the tank in the morning, that one or more of the smaller fish had found the water outlet while swimming in the night, and had slipped to the floor. They would be tightly coiled on the cool, moist cement floor, and were as agile and active there as in their native element.

There is one condition, however, that the fish cannot endure: a rise in temperature. The water on the surface of the Bay of Monterey averages in summer 64° F. or 17.7° C. What it is at a depth of two hundred feet, I do not know, nor how cold it gets in winter. But the air at Monterey is never so cold as to kill palms or heliotrope, so the water cannot become very cold. The water in the tank in which I kept the fish averaged 22° C., and in that they throve. On a warm sunny morning, I placed two young hagfish in a tank about three feet long by one foot wide, covered them with about five inches of fresh salt water at 22° C., and placed the tank by a window, where the sun shone directly into half of it, leaving the other half of it shaded. Under the heat of the sun the water in the tank rose gradually to 30° C. As the water became warmer, the fish grew very restless and languid, swimming constantly, not rapidly as usual, but with a slow, jerky movement as though seeking to escape the warm water. At the end of two hours and a half one of

them was lying almost straight. Both were put into the small aquarium with running water at a temperature of 22° C.; they swam freely for a few minutes, then settled down against the outflow pipe, having regained their normal habit. This was between half-past twelve and one o'clock. It was an exceedingly warm day, the thermometer standing at 89° F. in the shade, and the aquarium was so placed that the afternoon sun streamed directly upon it. About five o'clock I noticed that the two hagfish were very languid and stretched almost straight. On testing the water I found that it had risen to 29° C. Suddenly, the hagfish, without anything being done to disturb them, began to swim in a very violent, jerky way, and to throw out strings of slime, which is never done except when they are irritated. They would swim and stop intermittently, always lying at full length when at rest, and swimming so irregularly and violently as to injure themselves. When put into cooler water, 22° C., they immediately settled down quietly, half stretched out. I placed them in a small wooden tank in the cellar, by the large tank, in order to keep them separate from the other fish for a while, and note what after-effects there might be. The next morning one of them had escaped to the floor, together with two from the large tank. Of these three, two were entirely normal, and one was dead, in all probability the one that had been exposed to the heat the day before. The other hagfish grew steadily more languid, and died at noon the next day, two days after the experiment. Both fish were in a normal condition when the experiment began. It was positively the heat from which they suffered, and not the actinic rays, because they had been exposed to brilliant sunshine every afternoon for a month, and no ill effects had followed. The day they were affected was the first day there had been a marked rise in temperature.

Taken as a whole the hagfish do not lead an active life. When thoroughly aroused and on the alert, they swim at a very high speed, with a graceful, serpentine motion, but for the most part, they lie placid, perhaps motionless, perhaps lazily moving their heads from side to side. They are more active by night than by day. In the daytime more than once I found some of

them asleep. There was no outward difference between the sleeping ones and the others; all were curled quietly on the bottom, but if by chance a sleeping one was touched, instead of wriggling away it remained passive, unless perchance it coiled tighter, retaining its coil even when lifted from the water. Once I found two sound asleep, surrounded by a mass of slime in which they had in some way become lodged. The slime served them as a buoy, and they were floating quietly in it on the surface of the tank, circling around with the current. I took them out and stripped their covering from them, but they hardly aroused while I did so, and settled down to sleep again as soon as they were put back into the tank. Sometimes after a minute or two of handling they awake, but an interval elapses between their first stirring when they squirm uneasily in the hand, and full alertness when they swim rapidly away, or if held tight, they make the usual vigorous efforts to free themselves. If before the fish is wide awake, it is put back gently, it can drop off to sleep again. I once lifted a sleeping fish, dropped it into a pail, carried it a distance of more than two hundred feet, took it out of the pail, and started to decapitate it. All this motion followed by the tight grasp of my hand and the first touch of the shears, usually the first signal for the most frantic struggles, did not rouse it perceptibly, and its head was off before it began to squirm.

It is interesting to watch their movements, while they are becoming accustomed to confinement. When the first lot of fifty were placed in the tank it contained only water. They were normal fish in every respect and when first placed in their new home they swam around very vigorously, threw out a great deal of slime when touched, and were on the whole, unusually excited. After a short while, they settled down on the bottom, in the usual coils (Fig. 2), an occasional group of three or four together, the rest separate. Two days later sand was put on the bottom, and the rock pile built at one side. In a few hours all had burrowed among the rocks. There they lived very quietly, seldom moving when left to themselves, except at night. For the first four or five days they were easily aroused by dipping a small pailful of water from the tank and pouring it on

them. When this was done they would throw out great quantities of slime, and wriggle among the rocks, some of them leaving the nest, and swimming rapidly around the tank. When the sixth day came it was harder to rouse them, and for about ten days following they could hardly be stirred, neither throwing out slime nor swimming when the water was troubled. If one was lifted on a stick and moved, it quickly settled down wherever it might be, finding its way back to the rocks later. This was not due to illness, for their positions were normal. Toward the latter part of the third week, they became more active, lying quietly in the rocks when undisturbed, but rousing easily and getting much excited when water was poured on them from a pail, swimming freely and throwing off slime again, as they had done at first.

The second lot I received went through the same stages of liveliness and torpor as the first, and in about the same time intervals.

The so called slime they throw off is their chief means of protection. It often enables them to escape from whatever would catch them, by forming a covering so slippery that it is difficult if not impossible to get or keep hold of them. The thread cells are not emitted except upon sufficient provocation. I have often lifted them carefully and had them slip through my fingers without causing thread cells to escape. It is their response to conditions that irritate; they are always thickly surrounded with slime when caught on the hook, and the occasional ones that died natural deaths in the tank had always thrown off a considerable amount of slime in dying.

The question of what and how the hagfish eat, is one that has been much discussed in previous papers about them, some writers maintaining that they are parasites, and all stating that they are extremely voracious. In regard to this latter point the evidence comes from the fishing grounds. When the night lines are examined, one third or more of the hooks hold hagfish and the fish on many of the others have been entirely eaten away, nothing but the skin and bones being left. The hagfish has bored inside the skin and eaten all the soft parts, and is sometimes caught in the very act of wriggling away at the close of

its meal when the fish is taken from the water. From what I saw of their behavior in the tank, though, I conclude that this behavior shows the inordinate numbers of the fish in the bay, rather than extreme voracity. Those that I had were small feeders, and went a long time without eating. As a matter of fact, they ate so infrequently that I was not able to experiment with them and test their likes and dislikes as much as I wished.

According to the fishermen, the best bait is squid; failing that, they use herring, or as they call them, "sardines."

My first lot was caught on a Friday. The following Monday I put into the tank eight dead flounders about ten inches long and three inches wide. About a dozen of the fifty hags ate freely, some of them ravenously. But although several of the flounders had been partly eaten, the total consumed did not amount to more than two flounders.

It is very interesting to see them eat. The process may be easily watched when they are fed with small fish, or are just beginning on a large one. The feeding apparatus, described by Ayers and Jackson (:00), consists of a heart-shaped plate composed of symmetrical halves that open out and fold together like the leaves of a book. This plate bears on the dorsal surface of each half a double row of horn teeth, their points directed meso-caudad, and it lies imbedded in the membrane of the ventral wall of the pharynx.

When the animal feeds, the tooth plate, which is really a modified and movable lower jaw, and in no sense a tongue, as stated by Müller ('34) and P. Fürbringer, is thrust out of the mouth, and its fore end is drawn down so that it takes a position almost perpendicular to the long axis of the body. The two halves are at the same time drawn apart, so as to present an almost flat surface. Placing this flat surface against the fish to be eaten, the hag draws the halves of the tooth plate together, thus tearing off a portion of the food, and then withdraws it into its mouth. It swallows the food very rapidly, and immediately sticks out the tooth plate for more. There is no sucking motion as Fürbringer has said; the hagfish simply rests with its nose against the fish, and if, because of a current in the water, or through the vigor of the attack, the food is moved from its

position, the hagfish swims rapidly after, keeping in this way in constant touch with it.

This tooth plate is worked by five muscles, three of which form a unique mechanism called by Dr. Ayers the "club." These muscles lie close to the ventral surface and may all be seen when the ventral skin and body musculature are deflected back. The two that do not belong to the "club," lie ventro-cephalad of it (Fig. 3). The more lateral one arises as a narrow

Fig. 3.

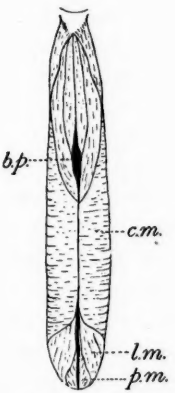


Fig. 4.

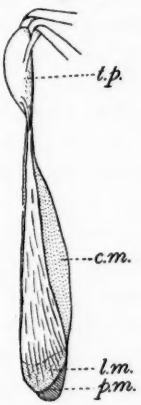


FIG. 3.— The "club muscle" and its accessories. Ventral view. *b. p.*, basal plate; *c. m.*, circular muscle; *l. m.*, long muscle; *p. m.*, perpendicular muscle. ½ natural size.

FIG. 4.— The "club muscle" and its accessories. Lateral view. Half of the circular muscle has been cut away in order to show the long muscle. *c. m.*, circular muscle; *l. m.*, long muscle; *p. m.*, perpendicular muscle; *t. p.*, tooth plate. ½ natural size.

band of fibers along the lateral edge of the cephalic half of the caudal section of the basal plate, runs cephalad, then curves slightly mesad, joining its fellow of the opposite side in a common aponeurosis, about a quarter of an inch behind the mouth opening. The aponeurosis continues forward until it reaches the mouth opening, where it fuses with the connective tissue which supports the mucous membrane of the lower lip; here it divides, each half deflecting posteriorly and laterally, to attach itself near the cephalic border of the tooth plate. The contraction of this muscle helps the two halves of the tooth plate to close together.

This mandibular muscle (Figs. 3, 4), is called by Fürbringer, m. copulo-glossus superficialis, and by Müller, "der oberflächlicher Vorzieher der Zunge." Both of these names are now inadmissible, as we are dealing with the lower jaw and not with the tongue as these authors thought.

Mesad of this superficially placed mandibular muscle lies Fürbringer's m. copulo-glossus profundis, Müller's "tiefer Vorzieher der Zunge." This muscle (Figs. 3, 4), consists of a lateral and a mesial division which join together at the cephalic end. The lateral division arises from the lateral edge of the caudal end of the third section of the basal plate. Its fibers run laterally, then curving, run cephalad along the border of the mandibular muscle last mentioned. The mesial division also arises from the lateral edge of the third section of the basal plate, between the points of origin of the lateral division of this muscle and the superficial mandibular muscle. It runs forward between the lateral division and its fellow of the opposite side, being separated from the latter merely at its hind end. The combined mesial and lateral divisions of each side fuse together at the cephalic end into a common tendon for the two muscles. This tendon runs cephalad between the basal plate and the aponeurosis of the superficial muscle, turns dorsad at the cephalic end of the latter, and runs caudad to the tooth plate where it divides again and is inserted midway in the length of the latter, close to the median line. This muscle, by contraction, draws the tooth plate forward, and by contracting to its full extent pulls it out of the mouth and into the vertical position.

The other three muscles that manipulate the tooth plate form a structure aptly named by Dr. Ayers the "club muscle." This "club" is between three and four inches long and consists of a hollow circular muscle, a long muscle, and a perpendicular muscle.

Of these three, the long muscle (Fürbringer's m. longitudinalis linguæ, Müller's "innere Längsmuskel der Zunge") is the only one in direct connection with the tooth plate. This long muscle (Figs. 3, 4, *l. m.*), is about three inches long, and from half to three quarters of an inch across its caudal end, tapering at its cephalic end to two tendons, one of which lies enclosed within

the other. These two tendons run cephalad to the tooth plate, just before reaching which they separate, the outer tendon attaching itself to the ventral surface of the tooth plate along the median line, the inner one dividing into two which curve laterad, run ventrad of the plate, and insert near the lateral border. The fibers of the long muscle are directed longitudinally. Shortly before reaching the caudal end, they separate into two divisions, permitting the passage between them of the perpendicular muscle. They curve around this, curve mesad toward each other, and end in a thin fascia that forms a partition between them. When this long muscle contracts, it draws the tooth plate back into the mouth, and then flattens it out again.

But as the long muscle is fixed only at one end, it cannot contract without assistance, hence the perpendicular and circular muscles.

The perpendicular muscle (Müller's "innere senkrechte Muskel der Zunge"), is a short rather stout muscle, arising from a small cartilage on the ventral surface of the "club," and running cephalo-dorsad, where it ends in a bounding fascia (Figs. 3, 4, *p. m.*). This little muscle, surrounded as it is by the long muscle, acts as a fixed point for the latter to contract around, and by contracting itself, increases its diameter as a pillar, and by thus taking up more room, helps the other to contract.

The circular muscle, also one of the mandibular muscles (Fürbringer's m. copulo-copularis, Müller's "höhler Aussermuskel der Zunge"), is a hollow cylinder surrounding the long muscle (Figs. 3, 4, *c. m.*). It begins about a quarter of an inch caudad of the tooth plate, and continues to within half an inch of the caudal end of the "club." It is much thicker at its cephalic end, where the long muscle consists of little more than a tendon, than at the caudal end, its walls growing thin there, and the long muscle increasing in girth. It is covered with an aponeurosis into which its fibers are set. Its fibers run circularly at right angles to the long axis of the "club." In cross section the walls of the circular muscle are seen to be crescent-shaped, thick on the ventral surface and at the sides, but thinning as they proceed dorsad, until only a thin layer or fascia is left to

close the cylinder upon its dorsal surface (Fig. 4). The circular muscle by contracting around the long, forces it back to where it has more room in the hind end of the "club," and so helps it to withdraw the tooth plate. Considering the extreme cumbersomeness of this device for using the lower jaw, it is rather remarkable that the hagfish can move it with the lightning-like rapidity with which it does.

If the fish is large enough to permit of it, the hagfish makes only one opening in the skin, and pushing in through that, works its way around inside, eating as it goes. I have seen three hagfish attack one fish through the same opening, their heads entirely hidden in the fish's body, their tails flapping like streamers in a wind as they pushed the fish in front of them, each striving to outdo its neighbor. They usually eat together, and I have often seen several of them at work on one dead fish, while other fish would be lying untouched in the aquarium. Under these circumstances it is no longer permissible to hold that the large fish found to be reduced to skin and bones, have been thus denuded by a single hag, though it may well be that only one of the number is detected in the act of leaving it.

The hagfish do not eat often. After the first feeding in captivity, a week passed before they were given anything more. Then flounders were given again, but only half a dozen ate. A week later, when flounders were offered them for the third time, only three touched them. At the end of another week they were given a rock cod, but did not touch it. Four days after, they were given a small cod and two small flounders, but did not touch them. It was not that the food did not suit them, for they eat any fish on the lines; they were evidently not hungry. Still I thought I would see if a different kind of food would tempt them more, so the next week, thirty-five days after they were caught, and seventeen days since any of them had touched food, and about a month after most of them had fed, I gave them five sardines, very flat fish, about eight inches long and two inches broad. There were about thirty hags in the tank, and by this time most all of them seemed to be hungry, for they ate all but one of the sardines. This was the only time ravenous hunger was observed during the summer. The

moment the first sardine was thrown into the water, the hagfish near it woke up, and went to it; other fish were thrown in, and in a minute or so the whole tank was alive. They ate ravenously, five or six crowding each other around one sardine. Within a few moments, twenty-one and a half of the two dozen sardines had been disposed of; the rest they finished during the night. As they seemed to be hungry, six sardines were given them four days later. The first was placed in the water very quietly and with as little jarring as possible; I had already noticed that an object could be placed quietly in the water without their paying any attention to it. When this first sardine was put in, however, several fish within six or eight inches of it were instantly on the alert, showing that they smelt it. They swam over to it, nosed around it, and ate a little. In a minute or so several fish at a greater distance stirred and came over, and they too nosed around the sardine. Other sardines were then thrown in, but comparatively few of the fish ate, and these only lightly. Although there were more than one hundred hagfish in the tank, only two and a half sardines were disposed of.

They were not fed again for two weeks and a half. Then seven sardines were given them. They woke up instantly and examined them, nosing around them as a dog does around a bone. About a dozen gnawed the fish in various places, and by the next morning three of the sardines were entirely eaten, but the others were untouched.

Of course in making these observations it was impossible to tell which fish fed at the different times, and how long any one fish went without food. But the day after the two dozen sardines were eaten, two fish were taken upstairs and placed in the small aquarium there, where they were kept for a month. During this month a sardine was offered them twice, and left with them for thirty-six hours, but was untouched on both occasions. It is thus apparent that they can go a long time without food, and do not eat nearly so heartily when they do feed as has been supposed. The explanation of the greater hunger of those freshly caught probably lies in the fact that they were rather hungry when they found the food in the trap, and that some of them had not been able to get enough of it to satisfy them.

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The question of parasitism can, I think, be answered fully in the negative. There is nothing in their structure to indicate degeneracy, either of the feeding organs, or of the senses with which they search for food. Moreover, they have no means of attaching themselves to living prey, unless that prey is held helpless on a line or in a net. They have neither hooks nor a sucking disc with which to hang on, and the palatine tooth is too short and placed too far back in the mouth to be used for this purpose. They can only swim and bite, and I hardly think they could make much headway with a powerful free-swimming cod or halibut.

There is one food, however, of which the males are extremely fond, and that is the eggs of their own kind. They eat these in great abundance, swallowing them whole. One evening, just before leaving the laboratory, I found a dead fish in the tank. It was a female with eggs almost ready for oviposition, and on lifting it the eggs were pressed out. I left them in the tank, twenty of them all told, to see what would happen. The fish had been fed the day before, and had eaten scantily, so they were not hungry, but by morning all but one of the eggs had been eaten; a day or so later I found the empty shells cast out. The egg is swallowed whole, and its contents slowly digested out of it by osmosis, leaving the shell untouched, or at most with only a prick in it given in passing over the teeth. I have examined several hundred eggs that had been pressed out from the intestine, and were in all stages of digestion, from the first murky clouding to the breaking and drawing off of the contents. In none of them was the shell really broken. In many of the largely digested ones there was no sign even of the pinhole prick, while in others quite undigested, the perforation of the shell was very evident. It must therefore be purely accidental and in no way necessary to digestion.

SENSE PERCEPTION.

The hagfish has all of the usual sensory nerves and sensory organs, barring the lateral line organs, possessed by the higher fishes, but they are all in a very primitive condition. It was

interesting by experiment to see what use was made of them. The eyes are not exposed on the surface, like those of other fishes, but are covered by the skin, which is, however, translucent for an area of about a square centimeter over them. There is nothing, therefore, to prevent the free passage of light. It has already been stated that when in the tank they would lie sometimes with their heads hidden in the rocks, but just as often with them projecting out into the light. It was suggested to me that this might be due to their wanting open water to breathe, and that possibly, other things being equal, they would prefer the dark. So to test it, two fish were placed in a large pan, three feet long by a foot wide, and half of the pan was covered making it very dark, while the other half was left open. It was a gray day, which made the light in the open end of the pan what they were accustomed to down in the tank. Both the fish were sluggish and did not swim much, but they were disturbed a number of times, and made to change positions. Each time when they settled down they seemed regardless of the light. They would settle quite as often at the light end of the pan as at the dark end. To make a surer test, two lively young fish were placed in a round dish about a foot in diameter and covered with an inch of water. After swimming rapidly for a few minutes, they settled down into tight coils. The dish was placed on the table in the photographic dark room, and a microscope lamp was lighted. The lamp had a light-tight iron chimney, with a curved glass rod coming out opposite the flame to concentrate the light on the disc at its far end. This disc was about a centimeter in diameter. The fish chosen were particularly valuable for the experiment because they were young and the skin over the eyes was unusually clear. In one of them it was transparent, so that I could distinctly see the eye beneath it. In the dark room the circle of light coming from the glass disc was held an inch above the water. It could as well have been at the other end of the room as far as observable results were concerned, for they paid no attention to it. It was moved closer and closer to them, finally being placed under the surface of the water, and within an eighth of an inch of their skin, without obtaining an observable reaction. At all of these differ-

ent distances, the light was moved so as to fall on different parts of each fish's body, eyes, tentacles, head, back, sides, etc., and there was no reaction to it by either hagfish.

In regard to whether they could perceive objects or not, the first thing that I noticed about them was, that when swimming rapidly in crossing the tank from side to side, they would repeatedly strike the tank head foremost; and when one was taken from among the rocks and held for some minutes in the hand or dropped in a corner of the tank, it would proceed very cautiously, moving its head from side to side, keeping its tentacles outstretched, and apparently depending on them for knowledge of its surroundings.

The two young hagfish referred to above I also tested for image perception, holding various objects close over their eyes, and bringing them nearer and nearer. They showed no reaction, no matter how near the object was, until the surface of the body was touched, when they jerked their heads away. These hagfish were neither sleepy nor sluggish, but were undoubtedly normal. The conclusion drawn is, that the perception of variations of light and shade even when extreme, does not irritate the eyes.

The evidence in regard to their hearing is just as negative as that concerning their sight. I was not able to find any noise or sound to which they would respond.

In testing the sense of touch, very different results were obtained. If the tank is jarred, the fish immediately tighten their coils; if they are touched suddenly they jerk their heads away. When they are swimming, and often when they are at rest, the tentacle crown is extended, and the tentacles, moving back and forth, sense the water currents or anything they may strike against. When swimming in search of anything, the tentacles are always on the alert, as tactile outposts or sentinels.

The same two fish that were studied for light perception, were also experimented on for touch, and were touched lightly in different places with a straw, a glass rod, and a fine needle. When touched lightly, fish A would not respond, but fish B would jerk itself away. Touching any part of the skin, whether of the head, over the eye, on the back, on the side of the body,

etc., gave the same reaction for each fish; A, as a rule, reacting less energetically than B. But if the tentacle of either fish was touched, the reaction was much greater, each fish jerking the tentacle sharply aside. There seemed to be no difference in sensitiveness between the base and the tip of the tentacles, and the fish responded the most of all upon being touched in the angle formed by the tentacle with the head. B jerked away when touched directly over the nose, but A did not notice it, and neither gave more attention to being touched over the eye-ball than in any other part of the skin.

In most cases when they react to the touch stimulus, they respond by curling the body tighter.

I placed a third young hagfish in the dish with the two, and then tried placing various liquids on or near them by means of a pipette. First as a control, I used ordinary sea water. When a stream of this was directed from a pipette against the tentacles and rim of the nose, they would draw the head a little to one side.

Ordinary alcohol was dropped in the water, one drop after another in front of B, within a half inch of the tip of its nose. Some of the drops touched it in mixing with the water, others did not. The contact of alcohol did not produce observable reaction until after twelve drops had fallen, when it moved away. When fish C was treated the same way, eighteen drops fell before it moved; the nineteenth touched it and it moved its head aside. B was touched again just as before, and again jerked its head away after the twelfth drop. The thirteenth drop placed in front of it at the usual distance, made it swim off to a different part of the dish. In this new position, eleven drops were given it one by one and it moved at the eleventh. C, treated a second time, took twenty drops before giving any reaction. The twenty-second made it a little uneasy; at twenty-three it moved its head slightly, and at twenty-four swam away. I followed it with another drop, and it went back to its old place. Three minutes later, it took five drops that all touched it in mixing. It quivered slightly at the third and fourth, but did not move aside until the fifth.

One drop of hydrochloric acid placed in the water near the fish

will make them jerk violently away if it touches them in any place while mixing with the water. A drop of strong ammonia does the same. The ammonia throws down a precipitate of ammonium chloride on the surface of the water, and if this drifts against them before dissolving they show extreme irritability. In all these cases it is largely the sense of touch that is affected, as the reaction was the same whether the mixing drop touched the tip of the tentacle, the rim of the nose, or the side of the head, and it was the touching of the mixture that produced the effect, except in the case of the alcohol, for it was found that when the visible mixture of the drop of acid or ammonia stopped even an eighth of an inch away from the fish, there was no reaction. With the ammonia this could be seen still more plainly, for wherever the ammonia was dropped, it was not until the ammonium chloride touched the skin, whether on tentacle, tip of nose tube, or skin at the side of the head, that the jerking away occurred. With the alcohol it was sometimes a drop that touched that caused the effect, sometimes not. With the many drops put in, only some of which touched the hag, and those not affecting it, it may be that the sense of smell was excited, or it may be that the alcohol finally irritated the mucous membrane lining the nasal tube, or possibly the skin of the tentacles. The foregoing experiments with the acid and ammonia were begun at half-past three o'clock, and were continued until five. By that time the eels had become very languid and were lying in the crescent shape. The next morning they were all right again.

Notwithstanding the negative results of these experiments in regard to the sense of smell, there is no question but that it is a most serviceable sense for the hagfish. As they cannot see, it is the means by which they know when they are near food. I cannot tell at what distance they can detect an object by the sense of smell. When the dead fish was placed in the tank, as stated above, and the hagfish within six inches were aware of it immediately, it took a perceptible time for those farther off to become so, but the scent reached those as far off as eighteen inches to two feet. How much farther it would go I do not know. It probably varies with different individuals.

I was not able to gather any data as to the sense of taste. So far as may be judged from observable reactions, the senses of touch and smell are the most important in the life of the hagfish. Watching its life for four months and examining its brain, both confirm this. Several times, to see what would happen, I took apart the rockery, transferring it to the other side of the tank. The hagfish, suddenly deprived of their place, were restless. First they moved their heads and the fore part of their bodies, groping around, and then began to swim. They swam in a slow, searching manner, sometimes feeling their way along the side of the tank, and always with their heads moving slowly from side to side, tentacles on the alert. Most of them, when they touched the rocks with a tentacle tip, would recognize them instantly, and go right in. Many on approaching within an inch or an inch and a half of them, would plunge straight for them, probably having smelt them. But there were others that, while searching, would glide directly over the rocks, perhaps even touching them with their bodies or the sides of their heads, or even with their tentacles, yet would give no evidence that they noted their presence; instead, they would continue their search farther afield, and eventually get back to them again.

On the other hand, they sometimes have a wonderful surety of motion. One morning I found one hagfish that had made a loop of its body, and was lying motionless, while three others were swimming through the loop, one after the other. They would dash through, describe a large circle from eighteen inches to two feet in diameter, come back to the starting point, and plunge through again. The hole in the loop was less than two inches across, and in the few minutes that I watched them, not one of the three hesitated, or failed to pass quickly and surely through the loop.

But they do not always carry sense of direction so well. If I took one away from the rocks, and dropped it immediately six or eight inches off, it generally went straight back. But if I held it a minute or so, or dropped it farther away, it would have to search for its resting place. Sometimes it would search and find it; sometimes, not finding it immediately, it would swim slowly around and settle down.

In other ways there is a difference in sensitiveness in the hagfish, showing in the varying strength of the reaction caused by different stimuli. The difference in the two fish with regard to the alcohol was one of these. At one time when two healthy fish were in the small aquarium, I struck the table on which the latter stood with a heavy iron bar, thus giving the aquarium a decided jar. The fish responded by tightening up their coils at the tail end, and then loosening them again, one fish reacting more strongly than the other. I pounded regularly at intervals of about five seconds, and they responded each time, the one always in a slightly more marked degree than the other, but the responses getting less and less, until at the twelfth blow they were no longer given. Half an hour later, when they were lying quietly, I tried again. This time they stopped at the eighth pound. The next day they were apparently more irritable, for they were still responding at the twentieth blow.

Their movements of defence are interesting. When caught, their efforts of escape are purely of the reflex order, trying to slip out of what is holding them. They wriggle and squirm to get away, throwing out their heads and wrapping their tails about one's wrist, but they rarely bite. The tooth plate is a formidable weapon, but they seldom use it as such. Of all the five hundred and fifty hagfish handled last summer, but few snapped, and only one bit. This is in keeping with the experience of others who have handled them.

Their power of reflex action is very strong, and when the head is cut off the body wriggles as violently without the head as it could with it. It will wriggle of itself for several minutes after the head is off, and after it becomes quiet it will respond, if touched, for several hours after the beheading, two or three hours in any case, and with the younger, smaller fish much longer. A fish was stretched out and nailed to a board, and injected through the heart with methylene blue. Forty-five minutes later the head was cut off, and the body thrown into a pan. Two hours after this a second headless body was thrown upon it and the first squirmed and tied itself into a knot.

These reflexes are just as strong in the tail end of the body as in the head end. Once in trying to open a hagfish to remove the

ovary, the fish, although it had already been beheaded, squirmed so that it was almost impossible to operate. The body was cut in half in the hope of quieting it, by cutting through the spinal cord, but both halves squirmed as vigorously as ever.

The most remarkable case of all was that of a young hagfish eleven and a half inches long. It was beheaded before noon. At five in the afternoon its body was opened its entire length. As soon as the instrument touched it, it squirmed vigorously, tying itself into a knot. In ten minutes the examination was over, it was thrown into the ocean, and my attendant at once reported that on touching the water it swam away. It would be interesting to know how long its swimming continued.

In contrast with the spinal cord, the life of the brain cells is short, particularly those in the fore part of the brain. When the fish were beheaded, the brains had to be removed and put into the killing fluid within an hour or they were valueless for histological work.

Reproduction.

The hagfish have only one reproductive organ, a peritoneal fold hanging from the roof of the right half of the body cavity. When the eggs or sperm are ripe, the organ fills the entire right side of the body cavity, but after discharge, it is all absorbed except for a small matrix at the caudal end. In this stage the sex of the organ is distinguishable only by histological examination. It appears as a small thickly gathered frill, the outer edge of which holds a multitude of tiny spheres, the undeveloped ova or sperm spheres respectively. As the hagfish has no external marks of sex, in this stage it requires a microscope to distinguish between male and female animals. As the process of ripening proceeds, the frill becomes thicker, and extends cephalad, the spheres becoming more numerous and the ova growing ovoid in shape. The frill may extend possibly one third of the way cephalad, before its edge becomes thicker, or the sex apparent. I cannot state positively at what length this occurs, but by the time it has grown halfway along the cavity, the edge is at least double in thickness what it was

in the beginning, and the sex plainly marked, the eggs being ovoid bodies, about two millimeters long and the sperm spheres larger than before.

Only between twenty and thirty egg cells develop into mature ova during one cycle, many of those starting development being arrested when from two to six or eight millimeters long, and the other spheres failing to develop. Whether this applies to the sperm spheres could not then be ascertained. No new facts were observed relative to the question of hermaphroditism. This condition was not present in any of the relatively few fish examined by me.

The hagfish oviposits at all seasons of the year, but probably a great many more mature in the spring than at any other season; and I think that no individual deposits eggs more than once a year, perhaps not so often as that. Of those studied by me between July 1 and October 30, about half were in the resting stage where it was impossible to detect sex difference. Among the others I did not find any fully ripe male; of the females only two had reached maturity, and of these but one produced ripe eggs, while the other died from some unknown cause before the eggs were deposited. The eggs are easily felt through the thin body wall in handling the fish, and I had from ten to a dozen fish with very large eggs under observation for six weeks or more, but the time was not sufficient to bring more than the one fish to the point of ovipositing.

The supposition that the greater number of hagfish breed in the spring is also supported by the relative numbers of eggs found at different times of the year. Embryos can be found at any time in various stages of development, but most of those taken even in September are small.

Of thirty-seven embryos gathered between September 8 and September 15, eleven were too small to be taken from the shell, eleven more were less than 30 mm. long, six were between 30 and 40 mm., seven between 40 and 50 mm., one 54 mm., and one 65 mm. This last was evidently within a short time of hatching, as it swam freely when taken from the shell. During this same week only four recently hatched hagfish were brought in, and of these one was 60 mm., one was 80 mm., and one 83

mm. The fourth had lost the fore part of its head so that I could not tell its exact length. I was told by the fisherman that eggs in which blood vessels could be seen were not very numerous before September. Late in September I received several very mature embryos and newly hatched young, and also some eggs in which the embryo was not more than eight millimeters, and was told by the fisherman that if I wished some young about four or five inches long to send for them at Christmas time as they were most easily obtained then.

The eggs are difficult to find. They are almost never taken in deep-water dredging, even in beds where the fish are very numerous. The United States Fish Commission steamer *Albatross* was out for three months in the spring of 1904, exploring the bottom of the Bay of Monterey, and in all that time only one egg was brought up by the dredge. On the other hand, Mr. Frederick Woodworth told me that in dredging for molluscs on a mud bottom at a depth of from twenty to twenty-five fathoms, he had several times brought up hagfish eggs. He says also in answer to a letter of inquiry on the subject: "I find from the fishermen that they have taken strings of eggs in from fifteen to eighteen fathoms with their mesh nets in muddy bottoms; with trawls they have taken them in as deep water as thirty-five fathoms, always on muddy bottoms." The one set of eggs that was laid in my aquarium was laid on the sand bottom, though there were the rock heap and the bare wood for the fish to choose between. Under these circumstances it is certainly probable that the hagfish do not breed in their usual habitat, but seek shallower water and a soft bottom to do so. The explanation for this will be found in the food habits of the young.

In gathering the eggs, aside from dredging, advantage is taken of the fact that they are eaten by the males. The fishermen set traps or lines for the fish, and when they are caught, hold them firmly by the head with one hand and "strip" the body with the other, thus forcing out any eggs or newly hatched young, for these are also eaten. Under these circumstances, only a very small proportion of the eggs obtained are good for histological study, as most of them have been more or less digested. Even if they are sufficiently uninjured to use for his-

tological purposes, the embryo is generally so much hurt that it will not develop further but must be fixed at once.

Hagfish embryos are exceedingly slow in developing. The evidence pieced together from the eggs brought in and the statements made by the fishermen as to the seasons when certain sizes of embryos were most easily found, was confirmed by the development of the seven eggs laid in the aquarium.

The average egg when laid is about twenty-three millimeters long (though some are shorter by several millimeters), and about six millimeters broad at the broadest place. The opercular ring is three millimeters from the animal pole (Fig. 5, *a*). Very rarely a second ring is found at about the same distance from the vegetal pole.

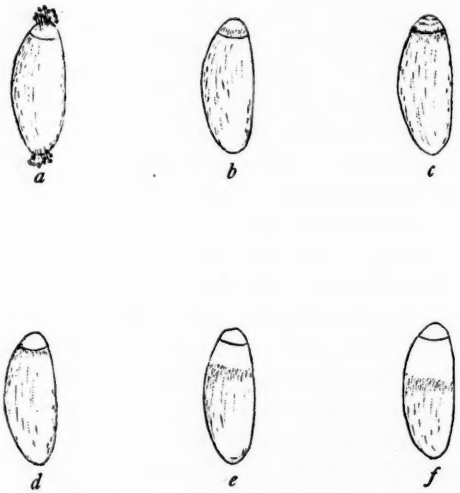

FIG. 5.— Eggs in the early stages of development. *a*, fresh laid egg; *b*, the same egg with the anchor filaments cut off, and showing protoplasmic disc at the animal pole; *c*, three-day egg, showing the terraces; *d*, at the beginning of the fourth day; *e*, the fifth day; *f*, the sixth day. Natural size.

Dean ('99) speaks of the egg being encased, when deposited, in two outer membranes, both of which are shed shortly after laying. Several eggs were brought me by the fisherman that had evidently been secured before they were ripe for oviposition. These eggs were identical with those, mentioned above, that I

had obtained from a hagfish which died in the aquarium. They were covered, anchor filaments and all, with a tough white membrane, translucent, but not transparent. When this was stripped off there was no second membrane inside, but instead, a thick jelly-like substance that filled in all the space between the egg-shell proper and the outer membrane. I do not hold with Dean that this outer membrane and jelly is shed shortly after laying, but think, instead, for two reasons, that the egg is freed from it before being deposited. The set of eggs in this condition taken from the dead fish, was left in the aquarium, and all but one were eaten before morning. That one, however, was left untouched. It had its outer membrane still on it, and remained in this condition. My second reason is, that the eggs normally laid in the aquarium, seven of which had been undisturbed, were, when I first saw them, entirely free from any such structure. They were in two groups, a group of four and a group of three, joined together by their anchor filaments and forming two parallel straight lines. There were no cast off membranes anywhere to be seen, and whatever might have happened to the jelly, the membrane could not have been dissolved by the salt water. Moreover, the eggs were joined by the anchor filaments, which could easily have happened if they were deposited free of membrane and jelly, but would have been impossible otherwise, as there was no force in the tank that could have changed the position of the eggs after they were deposited, or could have arranged them in regular groups. If the membranes were cast off after extrusion, what became of them? If they dissolved (and the one on the egg of the other set was neither dissolved nor cast off), how were the eggs pushed close enough together for their anchor filaments, previously separated by at least two thicknesses of membrane, to interlock?

I transferred the seven recently deposited eggs to a dish, in which was a constant flow of fresh salt water, in the hope that some of them might prove to be fertilized. The fresh eggs were a delicate, brilliant yellow in color with a white mass at the animal pole. I found them Tuesday morning, September 20th. Fig. 5, *a*, shows one in its normal state; *b* is the same egg without the anchor filaments, and shows the protoplasmic mass.

In the evening of the same day, two eggs, *a* and *b*, showed this protoplasmic mass extending halfway between the animal pole and the opercular ring. On the next day *a* had this mass extending two thirds of the way to the ring, while *b* was apparently unchanged. No changes had been noticed in any of the other eggs. Thursday showed no particular change in any of the eggs. On Saturday morning, the fourth day, *a* had a translucent cap, lighter in color than the rest of the egg, extending from the animal pole to one millimeter past the ring (Fig. 5, *d*), while in *b* the protoplasmic mass at the pole came two thirds of the way toward the ring, and was grouped in three distinct terraces (Fig. 5, *c*). The other eggs had merely the protoplasmic mass, coming halfway to the ring.

By three P. M. the same day, the cap of *a* had grown 1 mm. measuring 5 mm. from the pole to its edge at its deepest place. Before noon the next day it had grown 2 mm. more, measuring 7 mm. all told. Egg *b* had lost its terraces, and gained instead a cap, coming to within $\frac{1}{3}$ mm. of the ring, while a third egg, *c*, which had heretofore appeared quiescent, showed a marked terrace. One hour later the cap on *b* had passed the ring by $\frac{1}{3}$ mm. At this time *a* is represented by Fig. 5, *e*; *b* by Fig. 5, *d*; and *c* by Fig. 5, *c*.

Monday, the sixth day, at ten A. M., the cap on *a* was 9 mm. deep, and on *b*, 5 mm.; *c* was still in the terrace state, and terraces were showing faintly on *d*; *a* also had a tiny white dot, 1 to $\frac{1}{2}$ mm. below the ring, and in the middle of the flattened part of the egg. That same day at five P. M. the cap of *a* measured 9 mm. and the white speck was just the same, *b*'s cap was 6 mm. deep, the terraces of *c* and *d* were unchanged, and terraces were beginning to show on *e*; *f* and *g* were as they had been in the beginning. By measuring carefully morning and evening for several days I found that the average rate of growth of the cap after the terrace state was passed, was two millimeters in twenty-four hours, and that the time of highest rapidity was between ten A. M. and five P. M., as much space often being covered then as was covered between five P. M. and ten the next morning.

Tuesday, *a* and *b* were progressing at the usual rate of growth,

c had a cap reaching a little more than a millimeter past the ring, and *f*, in which I had not previously noticed any terraces, had a cap a trifle deeper than that of *c*. The caps in the earlier stages are very hard to detect, as the difference in translucency between them and the rest of the egg is very slight, and the shell somewhat opaque.

Wednesday morning at the end of the first week, *a*'s cap was 13 mm. deep, *b*'s 9 mm., *c*'s 7 mm., *f*'s 8 mm., while *d*, which had shown terraces almost as soon as *c*, lagged behind with a cap of only a little more than $4\frac{1}{2}$ mm.

By five P. M., *a*'s had grown 1 mm., *b* had not changed at all, while on the others the caps had grown 2 mm. each, twice the usual amount. That night, however, they all grew at the regular rate. Meantime, the white speck on *a* was no longer visible. On Friday, the tenth day, in addition to the usual increase in size of the cap, a very fine white line appeared on *c* a little below the ring, whose further history could not be traced.

On Monday, October third, at five P. M., not quite fourteen days after the eggs were laid, the blastopore of *a* was closed. Within a few days the blastopores of the other developing eggs closed also. Within this week, owing perhaps to very hot weather, the eggs died.

But they had lived long enough to confirm the idea of their exceedingly slow growth: fourteen days from the beginning of development to the closure of the blastopore, and no head elevation, or primitive streak showing in this time. In all eggs where the primitive streak shows, or where the young embryo does not extend the full length of the egg, there is a cap over the egg, that extends about one millimeter beyond the tail of the embryo. This second cap, however, is caused by changes in the yolk. With the appearance and growth of the mesoderm, the yolk near the embryo and immediately beneath the shell becomes spongy and full of vacuoles in which lymph and blood spaces are laid out. This gives this part of the yolk a whiter appearance than the rest and so forms a cap.

It is worthy of note that the five eggs that began to develop were supposedly all fertilized at the same time; nevertheless, there was a difference of from one to three days in the starting

of development, and only one started immediately. How shall we account for the uneven rates of growth noticed in one or two eggs afterwards, for instance on the day when *b* did not grow at all, and the others grew twice their usual daytime amount? What caused *f* to lie apparently quiescent for several days, then omit the terrace state, or cut it down to a ten or twelve hours at most, instead of the thirty-six to forty-eight it generally lasts and then growing with a leap, outstrip its brothers *c* and *d*, and finally even *b*? The eggs were all kept under identical conditions, and the most marked variations were in those in the same dish. It would seem impossible for external conditions to affect one without affecting all the others, yet here were decided variations in a process generally much more uniform.

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CINCINNATI, OHIO.
April, 1905.

NOTES ON THE GENITALIA OF LYMNÆA.

FRANK COLLINS BAKER.

Introduction.

With the exception of *Lymnæa megasoma* and *Lymnæa mighelsi*, nothing has been published on the genitalia of the American species of Lymnæa. Last fall the writer embraced the opportunity to dissect most of the common eastern Lymnæas, with some interesting results which are presented in the following paper.

In studying this subject it is eminently desirable that the material should be freshly killed and not alcoholic, as the latter condition causes portions of the genitalia to contract and otherwise lose their normal shape. Likewise in observing the male organ it is essential that it should be fully inverted, otherwise the form of the penis-sac and the length of the penis will be much modified, as shown by the accompanying cut (Fig. 1). The genitalia of the nine species examined are comparatively uniform, differing principally in the form of the prostate and in the length of the penis. The vagina and uterus also show some modifications.

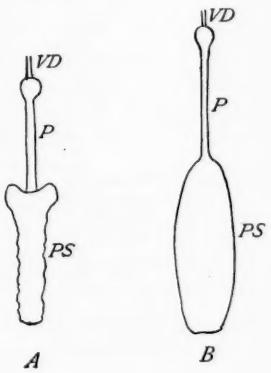

Fig. 1.—Male organs of Lymnæa. *a*, penis partly everted in penis-sac; *b*, fully inverted. Note the different shape of the penis-sac in the two conditions.

The material dissected was obtained from the following sources: *L. stagnalis appressa, stagnalis jugularis, elodes*, and *humilis* were collected in Braddock's Bay, Lake Ontario; *L. emarginata* and *catascopium* were collected

in Seneca Lake, N. Y.; *L. desidiosa* was obtained from Allen's Creek, N. Y.; *L reflexa* was obtained from Long Lake, near Millers, Indiana, and *L. auricularia* was secured in the greenhouse in Lincoln Park, Chicago. All but the last two were dissected in September.

In the figures the different parts of the genitalia are designated by the following letters: *al*, albuminiparous gland; *cm*,

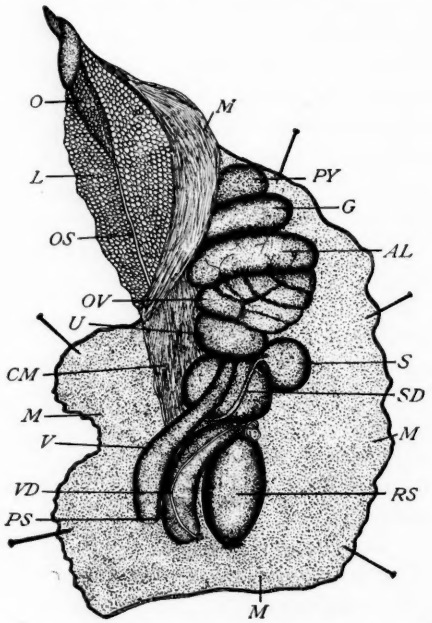

FIG. 2.—*Lymnæa stagnalis jugularis* opened from above, showing the reproductive organs in their natural position.

columella muscle; *fn*, nerves to female organs; *g*, gizzard; *l*, liver; *m*, mantle; *mn*, nerves to male organs; *o*, ovotestis; *ov*, oviduct; *os*, ovisperm or hemaphrodite duct; *p*, penis; *pd*, duct of prostate gland; *pr*, prostate gland; *ps*, penis-sac; *pmp*, penis protractor muscles; *pmr*, penis retractor muscle; *py*, pylorus; *rs*, radula sac; *s*, spermatheca or receptaculum seminis; *sd*, duct of spermatheca; *u*, uterus; *v*, vagina; *vd*, vas deferens.

The position of the genitalia is the same in all of the species

examined, the male and female organs opening by separate orifices, that of the former being behind the right tentacle and that of the latter at the base of the neck, not far from the pulmonary opening. The genitalia occupy the median portion of the body cavity and are the most conspicuous organs when the animal is opened from the back (Fig. 2). The female organs closely embrace the alimentary tract, stomach, and esophagus, the ovotestis being imbedded in the liver near the posterior part of the animal. The male organs lie to the right of the buccal sac, the vas deferens being coiled up between these two organs. The relations of the different organs cannot be made out until they are spread out and separated from each other.

Discussion of Species.

Lymnæa stagnalis appressa Say. (Figs. 3, 4.)

Male Organs.— Penis-sac very large, cylindrical, rather wide at the external opening and narrowing toward the distal end where the penis is attached. The penis is very short and rather thick, about one fourth the length of the penis-sac. There are three sets of protractor muscles on the penis-sac and two sets of retractor muscles. A large, thick muscle is inserted in the head of the penis at one end and is attached to one of the retractor muscles. The vas deferens is very long and extends from the penis to the base of the penis-sac where it is lost in the columella muscle, to appear again at the base of the vagina as the duct of the prostate gland, which is long and hair-like and enters the prostate in a rounded, bulbous-shaped organ, which gradually narrows until it enters the ovisperm duct.

Female Organs. — The vagina is a narrow, cylindrical organ about as long as the penis-sac. At the distal end it forms a large, rounded, more or less pyriform uterus, which narrows to form the oviduct, which is a tortuous, much folded organ, doubled upon itself several times. This organ narrows and unites with the ovisperm duct, which leads to the ovotestis or hermaphrodite gland, which is made up of rounded or lobulated follicles and is strongly attached to the liver. The albuminiparous gland

is very large. The receptaculum seminis is rather small, pyri-

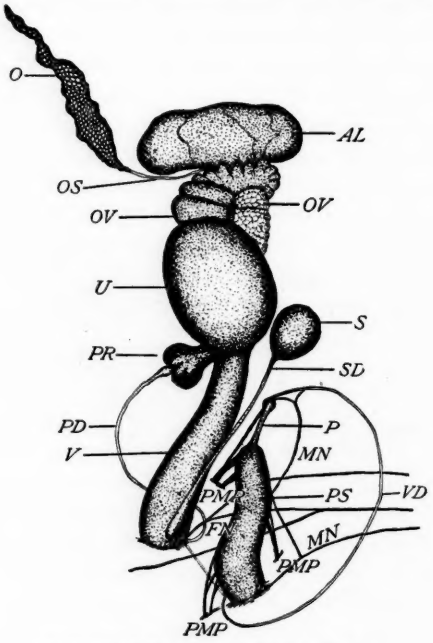

FIG. 3.—Genitalia of *Lymnæa palustris appressa.*

form, and is connected with the lower part of the vagina by a long, narrow duct. Both male and female genitalia are supplied with nerves, the former from the cerebral ganglion and the latter from the right visceral ganglion.

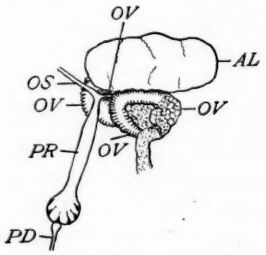

FIG. 4.—*Lymnæa palustris appressa*, showing position of oviduct, prostate, and ovisperm duct.

The organs are very brightly colored, the albuminiparous gland, oviduct, uterus, and receptaculum seminis being orange, the prostate orange shading into black at its insertion, the vagina blackish white, and the penis-sac flesh-colored. The ovotestis is white, as are also the muscles, vas deferens, and ducts of the female organs. The ganglia are bright pink or orange.

The true relations of the hermaphrodite portions of the genitalia cannot be understood until the organs are separated and spread out, when it is seen that the ovisperm duct divides into two branches, one branch forming the prostate, which cares for the spermatozoa, and the other branch forming the oviduct which carries the ova.

Lymnæa stagnalis jugularis Say.

The genitalia of this variety are in all respects like those of variety *appressa* excepting in color, the prostate being brownish yellow, the receptaculum seminis yellowish white, and the rest of the female organs yellowish and flesh-colored.

Compared with the European *stagnalis*, the American varieties seem to be almost identical. The figures in Keferstein (Taf. 103, Fig. 8) differ only in the form of the uterus, which is represented as more pyriform, and the bulbous part of the prostate is larger. The penis is not clearly defined in the figure. The figure in Prasch (Taf. 5, Fig. 7) is almost identical, the male organs being shown in much detail. The uterus is somewhat differently shaped but this may be due to a different point of view. There is nothing in the genitalia to separate the varieties of *stagnalis*.

Lymnæa palustris Müller (= *elodes* Say). (Fig. 5.)

Male Organs. — The penis is almost as long as the penis-sac and is very slender. The penis-sac is rather long, cylindrical, and of large diameter. There are two large, wide, ribbon-like retractors attached to the penis-sac and one muscle from the head of the penis to the posterior retractor muscle. Protractor muscles similar to those of *stagnalis*. Vas deferens long and thread-like. Prostate duct very fine; prostate thick, cylindrical, connected with the ovisperm duct as in *stagnalis*.

Female Organs.— Vagina long, cylindrical, of narrow diameter, enlarging to form a large, thick, pyriform uterus which narrows to form the much folded oviduct, which in turn narrows to form the ovisperm duct. Albuminiparous gland large. Receptacu-

lum seminis very large and globular, its duct very fine, enlarging somewhat at the point of insertion near the opening of the vagina. Ovotestis and nerves as in *stagnalis*.

The colors of the organs are: albuminiparous gland and uterus bright yellow, receptaculum seminis and prostate yellow-

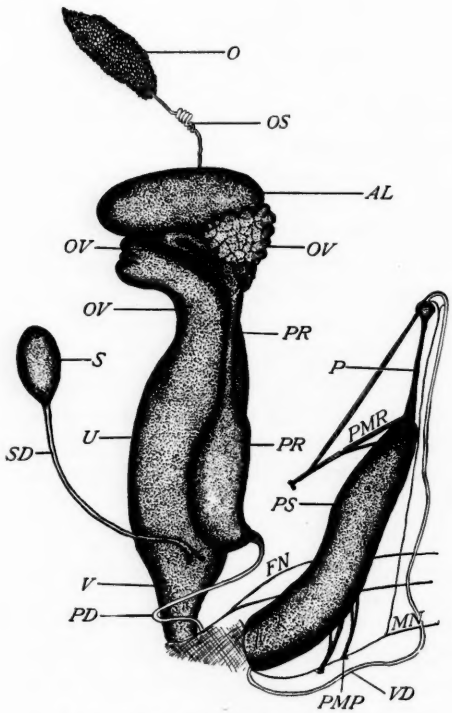

FIG. 5.—Genitalia of *Lymnæa palustris* (=*elodes*).

ish, penis-sac blackish, muscles, penis, vas deferens, and nerves whitish or flesh-colored.

Palustris differs from *stagnalis* in the greater length of the penis, has a larger receptaculum seminis, a more pear-shaped uterus, and the proximal end of the prostate is pyriform, not bulbous.

Lymnæa reflexa Say.

The genitalia of this species seem to agree in all essential characteristics with those of *palustris*. The penis-sac has but one retractor muscle while the penis has the long retractor inserted in this muscle as in *palustris*.

Lymnæa emarginata Say. (Figs. 6, 7.)

Male Organs.— Penis and penis-sac as in *palustris* and *reflexa*. A single penis-sac retractor muscle in which the penis retractor

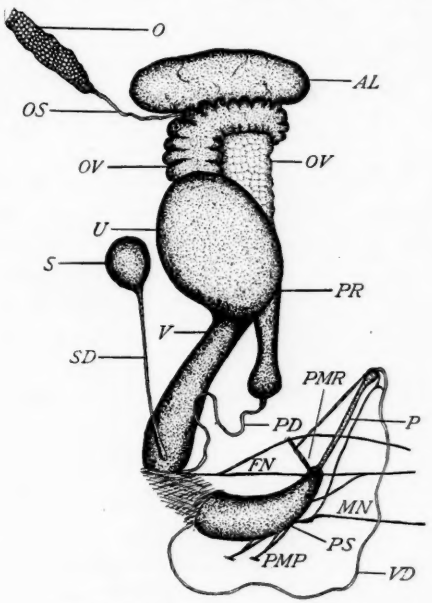

FIG. 6.—Genitalia of *Lymnæa emarginata*.

is inserted. Prostate cylindrical, of large diameter, with a somewhat bulbous proximal extremity, which narrows behind and then enlarges, to contract again before connecting with the ovisperm duct.

Female Organs.— The vagina is rather short and of large

diameter; the uterus is somewhat egg-shaped and very large; oviduct large and much folded. Receptaculum seminis globular, small, its duct very fine, inserted near the opening of the vagina. Albuminiparous gland large.

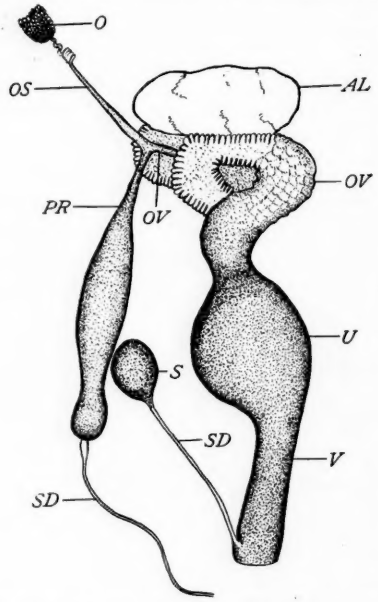

FIG. 7.— Genitalia of *Lymnæa emarginata*, the organs separated to show their relations to each other. Note the division of the ovisperm duct to form the oviduct and prostate.

The organs are colored as follows: oviduct orange, male genitalia blackish white, the rest of the organs flesh-colored.

The genitalia of *emarginata* differ from those of *palustris* in having a more bulbous-shaped uterus, a smaller receptaculum seminis and a more cylindrical prostate, which terminates in a somewhat bulbous enlargement resembling that of *stagnalis*. The muscles of the penis and penis-sac are like those of *palustris*.

Lymnæa desidiosa Say. (Fig. 8.)

Male Organs.— Similar to those of *emarginata*. The prostate is whitish and is irregularly fusiform, tapering at both extremities. Muscles and their insertions as in *emarginata* and *reflexa*.

Female Organs.— The vagina is very short and the uterus is large and long and pyriform in shape. The receptaculum seminis is globular in form and larger in proportion than that of *emarginata*.

FIG. 8.— Prostate of *Lymnæa desidiosa*.

Lymnæa humilis Say.

The genitalia of this small species appear in all respects like those of *desidiosa*. The receptaculum seminis is a rich salmon color, the prostate is whitish, and the rest of the organs are yellowish white.

Lymnæa mighelsi Binney.[1] (Fig. 9.)

Male Organs.— Penis-sac cylindrical, very long and of large diameter. Penis long and slender, half the length of the penis-

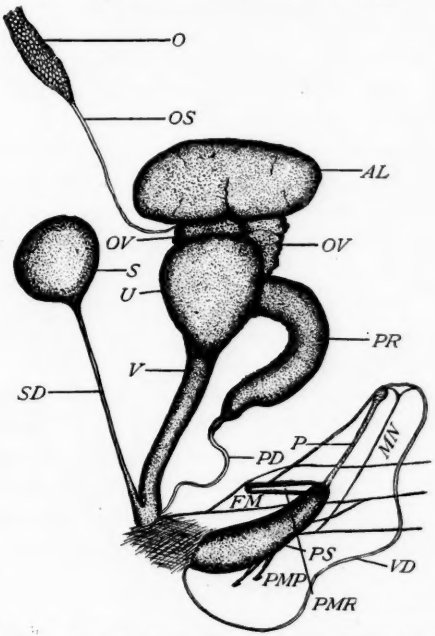

FIG. 9.— Genitalia of *Lymnæa mighelsi*. The male organs are drawn somewhat nearer the female organs than in nature.

sac. There is a single stout, ribbon-like retractor muscle attached

[1] The description of *mighelsi* is modified and corrected from that published in *Bull. Chicago Acad. Sci.*, vol. 2, no. 3, p. 202.

to the distal end of the penis-sac; and the penis muscle, which is attached to the head of the penis, is inserted in this muscle near its attachment to the columella muscle. Vas deferens and innervation as in the other species described. The prostate is large and cylindrical at its junction with the prostate duct, but becomes very long and narrow at its posterior portion and again narrows as it unites with the ovisperm duct.

Female Organs.— The ovotestis is made up of the usual lobulated follicles. The ovisperm duct is rather long; the oviduct is a much lobed organ, rather long and of large diameter; it enlarges to form a long, cylindrical uterus which suddenly contracts to form the vagina. The receptaculum seminis is small, elongate-ovate in form and connects with the vagina rather high up by a narrow duct. The albuminiparous gland is not large and is of the usual form. The innervation is as in the other species described.

The organs are colored as follows: penis and penis-sac yellowish, prostate yellowish or amber-colored, ovotestis yellowish, albuminiparous gland greenish, receptaculum seminis pearly white, and the other organs yellowish. The muscles are white in color.

The genitalia of *mighelsi* differ from those of all the other species described in the form of the uterus, which is long and cylindrical while the vagina is short and wide. The prostate is also differently shaped. The penis-sac is very long and wide while the penis is about half its length. It is evident from a study of the genitalia of *mighelsi* and *emarginata* that the former is specifically distinct from the latter. The penis is shorter, the oviduct is differently shaped, as well as the prostate. The shells also exhibit differential characters.

Lymnæa catascopium Say.

Male Organs.— In all respects like those of *emarginata.* The prostate is also like that of *emarginata.* The receptaculum seminis is more pear-shaped. The uterus is not so swollen, the distinction between vagina and uterus not being very marked, and the two organs form a long, somewhat cylindrical sac.

Lymnæa auricularia Linné. (Fig. 10.)

Male Organs.— Penis-sac cylindrical, long, of large diameter. Penis very long and slender, exceeding the penis-sac in length. Penis retractor single, attached to the distal end of the penis-sac by a double connection. Prostate in the form of an elongated, inverted pear, narrowed at either end where it joins the

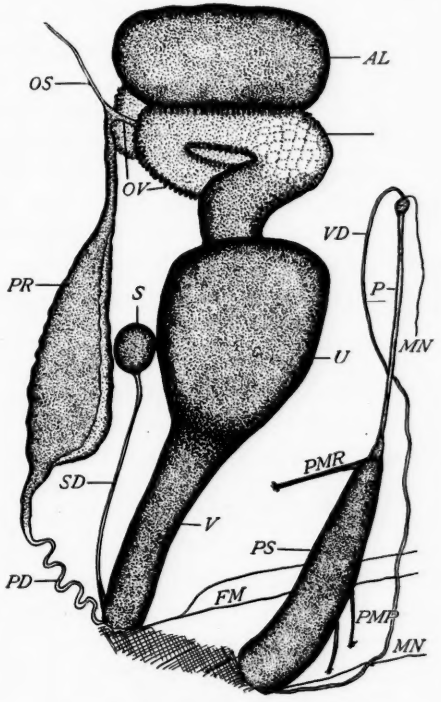

FIG. 10.— Genitalia of *Lymnæa auricularia*.

ovisperm duct and prostate duct. The prostate is dark gray in color with the exception of a narrow band of white on the border.

Female Organs. — The ovotestis is of the usual form. The ovisperm duct is of medium length. The oviduct is a much

lobed organ, rather long and wide; it abruptly enlarges to form a bulbous uterus, which narrows to form a rather long, wide vagina. The receptaculum seminis is small and spherical and connects with the vagina near its opening by a very long, narrow duct. The albuminiparous gland is very large. Nerves as in the other species. The uterus is yellowish, the albuminiparous gland is yellowish brown, the vagina is blackish white, the receptaculum is bright red and the other organs are flesh-colored.

The genitalia of *auricularia* do not resemble those of any other species very closely. The penis is longer than in any other species and the receptaculum is smaller. The uterus is more swollen and of a different shape. The prostate resembles that of both *elodes* and *mighelsi*.

Moquin-Tandon's figure in the *Histoire Naturelle des Mollusques Terrestres et Fluviatiles de France* shows the organs of different shape and position, but this may be due to viewing them in a different position and without separating the organs.

Lymnæa megasoma Say.

No specimens of this species have been obtainable for dissection. Wetherby's description and figure in *Jour. Cincinnati Soc. Nat. Hist.*, vol. 2, p. 95, show the penis to be rather wide and shorter than the penis-sac. The receptaculum seminis is ovate-pyriform. The other organs are not very clearly shown.

COMPARISONS.

The question has presented itself to the writer as to whether the genitalia of Lymnæa will afford sufficiently stable data upon which to base systematic groups or subgenera. In the land shells these organs furnish, in many cases, excellent characters for generic and even family divisions. It is possible that the examination of a large number of species might produce tangible

results, but the data presented in this paper seem hardly sufficient for this purpose, although some interesting features are brought out.

In the foregoing remarks, nine species and two varieties have been discussed. In comparing the genitalia of these eleven forms, several notable facts are at once apparent. The length of the penis as compared with the penis-sac is striking. The following table shows these relations (see Fig. 11):—

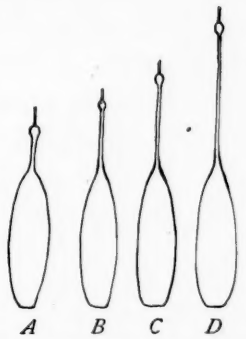

FIG. 11.—Comparison of the length of the penis with the penis-sac. *a, stagnalis*; *b, mighelsi*; *c, palustris*; *d, auricularia.*

Comparative Length of Penis and Penis-sac.

One fourth length.	One half length.	Three fourths length.	Longer.
appressa	*mighelsi*	*emarginata*	*auricularia*
jugularis		*palustris*	
		reflexa	
		catascopium	
		desidiosa	
		humilis	
		megasoma?	

There seems to be some difference in the number of penis retractor muscles attached to the penis-sac. In *stagnalis* and *palustris* there are two, with a muscle extending from these muscles to the penis. In *emarginata*, *mighelsi*, *auricularia*, *reflexa*, *desidiosa*, *humilis*, and *catascopium* there is but one retractor, in which is inserted the penis muscle. In *auricularia* there is but one penis-sac retractor and no muscle is attached to the penis. The prostate shows some differences, being fusiform in some species (*viz.*, *desidiosa*, *auricularia*, *mighelsi*, etc.) and cylindrical with an enlarged bulbous termination in the other species (*viz.*, *stagnalis*, *emarginata*). The uterus also varies from ovate to pyriform.

The colors of some of the organs, especially of the receptaculum, are striking. This latter organ is colored as follows in the different species : —

appressa, orange.	*desidiosa*, salmon.
jugularis, yellowish.	*mighelsi*, pearly white.
reflexa, yellowish.	*humilis*, salmon.
emarginata, flesh-colored.	*auricularia*, bright red.

The receptaculum seminis varies in several of the species, both in size and in shape. In *palustris* it is of extraordinary size while in *auricularia* it is very small.

While the characters of the genitalia do not seem to aid materially in the establishment of higher groups they do aid very largely in the separation of the species. The writer hopes to be able to examine all of the American species in the near future.

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'72. Du systeme nerveux des mollusques et d'un nouvel organe d'innervation. *Arch. Zool. Exp.*, ser. 1, vol. 1, pp. 437–500.

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'55. Histoire naturelle des mollusques terrestres et fluviatiles de France. Paris, 2 volumes and atlas.

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'61. Observations sur les prostates des Gastéropodes androgynes. *Jour. de Conch.*, vol. 9, pp. 1–19.

[1] The list of works on this subject is not exhaustive.

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'43. Neben das Geschlechtssystem und die Harn bereitenden Organe einiger Zwitterschnecken. *Arch. für Naturges.*, 1843, pt. 1, pp. 71–104.

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'79. Notes on some New or Little Known North American Limnæidæ. *Jour. Cincinnati Soc. Nat. Hist.*, vol. 2, p. 95.

WHITFIELD, R. P.

'81. Description of *Limnæa* (*Bulimnæa*) *megasoma* Say, with an Account of Changes produced in the Offspring by Unfavorable Conditions of Life. *Bull. Amer. Mus. Nat. Hist.*, vol. 1, pp. 29–37.

CHICAGO ACADEMY OF SCIENCES.

NOTES AND LITERATURE.

BOTANY.

Porter's Catalogue of the Bryophyta and Pteridophyta of Pennsylvania[1] is an attractive volume of 66 pages. It is a list in which localities and collectors are indicated after the name of each species, and includes about 542 species and varieties. The catalogue was compiled by Dr. Porter, the mosses revised by Mrs. Britton, and the whole edited by Dr. Small. The names of such well known collectors as James, Austin, Muhlenberg, Porter, Rau, Garber, Burnett, Small, and Mrs. Britton appear many times throughout the catalogue and add much to its value. The arrangement of families and genera conforms very closely with that in Limpricht's *Die Laubmoose.* Some exceptions to this statement will be noticed, *e. g.*, Hylocomium is placed between Brachythecium and Eurhynchium.

Some of the most conspicuous changes in familiar generic names are the following: Mollia Schrank for Gymnostomum (partly), Gymnostomum Hedw. for Pottia, Weissia Ehrh. for Ulota, Leersia Hedw. for Encalypta, Astrophyllum Neck. for Mnium, Arrhenopterum Hedw. for Aulacomnium (partly), Mnium Dill. for Aulacomnium (partly), Webera Ehrh. for Diphyscium, Eleutera Beauv. for Neckera, and Forsstromia Lindb. for Leptodon.

The catalogue is well bound in a very neat cloth cover and is clearly printed on good paper with a dead surface. It is absolutely indispensable to all students of the Pennsylvania Archegoniates and even the more general student should not neglect placing it in his library.

J. F. C.

Notes.— The seventh fascicle of the Genera Siphonogamarum of Dalla Torre and Harms, following the Engler sequence of families, has reached Liabum, of the Compositæ — which bears the serial number 9371.

Vol. 8, part 5, section 2, of the *Reports of the Princeton University Expeditions to Patagonia*, by Macloskie, deals with the phanerogamic families Santalaceæ to Cactaceæ, and bears date of January 2.

[1] Porter, T. C. *Catalogue of the Bryophyta and Pteridophyta of Pennsylvania.* Boston, Ginn & Co., 1904. 8vo., 66 pp. $1.00.

The new edition of the *Prodromus Floræ Batavæ*, in course of publication by the Nederlandsche Botanische Vereeniging, reaches the end of Apetalæ in the third part of volume 1, recently issued.

A second part of de Wildeman's studies of Congo plants has been issued from Brussels.

Vol. 5, part 1, of Wood's Natal Plants, dealing with grasses, is dated December, 1904.

"The Luquillo Forest Reserve, Porto Rico," is the title of *Bulletin no. 54* of the Bureau of Forestry, U. S. Department of Agriculture, by Gifford.

A paper by Shimek on the flora of the St. Peter sandstone in Winneshiek County, Iowa, is published in vol. 5, no. 4, of the *Bulletin* from the laboratories of natural history of the State University of Iowa.

A colored plate of *Shortia galecifolia* appears in *Flora and Sylva* for January.

A colored plate of *Yucca guatemalensis* is published in *Curtis's Botanical Magazine* of February.

An account of *Musa textilis*, by Edwards, forms *Farmers' Bulletin No. 12* of the Philippine Bureau of Agriculture.

A paper on the grasses of Walter's "Flora Caroliniana," by Hitchcock, has been separately printed from the *Sixteenth Report of the Missouri Botanical Garden.*

Dulichium spathoceum is said by Hartz, in Engler's *Botanische Jahrbücher* of February 28, to occur in Danish interglacial bogs.

An account of *Welwitschia mirabilis*, with original photographic illustrations taken in its native home, is published by Baum in *Die Gartenwelt* of March 18.

Professor Greene publishes a number of new species of Aragallus in the *Proceedings of the Biological Society of Washington* of January 20.

An account of the British Hieracia, recently published by W. R. Linton, includes 124 species with numerous minor forms.

Habit and bark photograms of *Fraxinus pennsylvanica* are published by Rothrock in *Forest Leaves* for February.

The 20th Heft of Engler's "Das Pflanzenreich" consists of a treatment of Zingiberaceæ, by Schumann.

No. 20 of the *Bulletin de l'Institut Botanique de Buitenzorg* consists of a paper on Javan Zingiberaceæ, by Valeton.

An epitome of the British Indian species of Impatiens, by Sir Joseph Hooker, is begun in vol. 4, no. 1, of the *Records of the Botanical Survey of India*.

Spegazzini records 140 cacti, of which many are described as new, from the Argentine Republic in a paper separately issued from vol. 11 of the *Anales del Museo Nacional de Buenos Aires* under the title "Cactacearum Platensium Tentamen."

A paper on Cephalotus by Hamilton, with other interesting botanical matter, is contained in vol. 29 of the *Proceedings of the Linnæan Society of New South Wales*.

Some West American red cherries are described by Greene in the *Proceedings of the Biological Society of Washington* of February 21.

A paper on the comparative anatomy and phylogeny of Abietineæ, by Jeffrey, forms vol. 6, no. 1, of the *Memoirs of the Boston Society of Natural History*.

Dr. Moore's Philadelphia address on "Applied Botany and its Dependence upon Scientific Research" is separately issued from *Science* of March 3.

Dr. Galloway's recent report as chief of the Bureau of Plant Industry shows in a concise way the varied investigations being carried on by this branch of the national Department of Agriculture. Sixty-one percent of the 490 employees of the Bureau are said to be engaged in scientific and related work.

A popular account of henequen farming in Yucatan is to be found in *Modern Mexico* of February.

A colored plate of the rose "Madame Norbert Levavasseur," which has been rechristened "Baby Rambler" in this country, is published in *Gartenflora* of January 1.

A monograph of American varieties of lettuce, by W. W. Tracy, Jr., forms *Bulletin no. 69* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

An instructive winter tree-study bulletin, for young people, is contained in the February–March number of the Cornell *Home Nature-Study Course*.

Some old British tree trunks are figured in vol. 22, part 3, of the *Transactions and Proceedings of the Botanical Society of Edinburgh.*

The deformations of woody plants sometimes called "witches' brooms" are discussed by Solereder in the *Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft* for January.

An account of graft-hybridization or symbiosis in Vitis is given by Voss in *Landwirtschaftliche Jahrbücher*, vol. 33, part 6.

The effect of self-pollination in Papilionaceæ is discussed by Kirchner in the January *Naturwissenschaftliche Zeitschrift für Land- und Forstwirtschaft.*

Seaside ecology in Ceylon finds exposition by Tansley and Fritsch in *The New Phytologist* of January 30.

An account of the Mandragora of the ancients in folk-lore and medicine, by Randolph, forms vol. 40, no. 12, of the *Proceedings of the American Academy of Arts and Sciences.*

The chemistry of indigo is considered by Hazenwinkel and Wilbrink, in no. 73 of the *Mededeelingen uit 's Lands Plantentuin*, from the Buitenzorg Garden.

A popular account of the seedless, coreless, and blossomless apples is given by Thomas in *The American Inventor* of April 1.

An interesting series of weed studies, by Waldron, constitutes *Bulletin no. 62* of the North Dakota Experiment Station.

Von Schrenk reports on experiments in the chemical treatment of railroad ties as a means of checking fungus growth, in *Bulletin no. 51* of the Bureau of Forestry, U. S. Department of Agriculture.

Professor Macbride's Philadelphia address, on The Alamogordo Desert, is distributed in separate form.

That the raphides of Agave, like those of *Scilla maritima*, Narcissus, etc., may cause severe irritation of the skin is noted in the *Gardeners' Chronicle* of March 11.

Roth's "Die Europäischen Laubmoose" has reached a conclusion in the recently issued 11th Lieferung.

An important contribution to the bryology of the Azores is published by Cardot in the *Bulletin de l'Herbier Boissier* of February 28.

The supposed influence of fungi in causing the formation of tubers in Solanum has been further tested, with inconclusive results, by

Jumelle, whose paper appears in the *Revue Générale de Botanique* of February 15.

Fusicladium pirinum, and its effect on the pear, form the subject of *Bulletin no. 163* of the Agricultural Experiment Station of California, by Smith.

Bæodromus, a coleosporioid rust of Senecio, is described by Arthur in *Annales Mycologici* of February, which also contains other papers on American fungi.

The Discomycetes of Iowa form the subject of a paper by Seaver in vol. 5, no. 4, of the *Bulletin* from the laboratories of natural history of the State University of Iowa.

An analysis of the species of Phragmidium, by Dietel, has been published in recent numbers of *Hedwigia*.

Atkinson's 1893 account of "Carnation Diseases" is reprinted in *The American Florist* of January.

A discussion of soil bacteria and nitrogen assimilation, by Chester, forms *Bulletin no. 66* of the Delaware College Agricultural Experiment Station.

A paper by Moore on soil inoculation for legumes, with reports upon the successful use of artificial cultures by practical farmers, constitutes *Bulletin no. 71* of the Bureau of Plant Industry of the U. S. Department of Agriculture.

A further discussion of copper as an algicide and disinfectant in water supplies is given by Moore and Kellerman in *Bulletin no. 76* of the Bureau of Plant Industry, U. S. Department of Agriculture.

A catalogue of the shrubs in the Vilmorin Garden, by Maurice L. de Vilmorin and D. Bois, with descriptions of new or recently introduced species, has recently been issued from the *Librairie Agricole* of Paris.

An illustrated account of the desert laboratory at Tucson is given by Lloyd in the *Popular Science Monthly* for February.

A Herkomer portrait of Sir Joseph Hooker is reproduced in halftone in *The Gardeners' Chronicle* of January 7.

A note on the work of Philippi, with portrait, is published by Hicken in the *Anales de da Sociedad Científica Argentina* of October last.

A portrait of B. L. Robinson is published in the *Popular Science Monthly* for February.

The Journals. — With January, a new journal, *The Nature Study Review*, appears under the editorship of Professor M. A. Bigelow with a strong advisory board. It contains much of interest to the teaching botanist.

The Iowa Naturalist is a new venture launched by T. J. Fitzpatrick from Iowa City.

An attractive new periodical, *The Garden Magazine*, is begun by Doubleday, Page & Co., the first number issued being for February.

Botanical Gazette, January: — True and Oglevee, "Effect of the Presence of Insoluble Substances on the Toxic Action of Poisons"; Livingston, "Relation of Soils to Natural Vegetation in Roscommon and Crawford Counties, Mich."; Elmer, "New and Noteworthy Western Plants"; Olive, "Morphology of *Monascus purpureus*"; Davis, "Fertilization in the Saprolegniales," and "The Sexual Organs and Sporophyte Generation of the Rhodophyceæ."

Botanical Gazette, February: — Barnes, "The Theory of Respiration"; Whitford, "The Forests of the Flathead Valley, Montana — I"; Holm, "Studies in the Gramineæ — VIII, *Munroa squarrosa*"; Chamberlain, "Alternation of Generations in Animals from a Botanical Standpoint"; Ganong, "New Precision-Appliances for Use in Plant Physiology — II."

Botanical Gazette, March: — Coulter and Land, "Gametophytes and Embryo of *Torreya taxifolia*"; Olsson-Seffer, "The Principles of Phytogeographic Nomenclature"; Whitford, "The Forests of the Flathead Valley, Montana — II"; Arthur, "Terminology of the Spore Structures in the Uredinales."

Muhlenbergia, no. 6. — Heller, "Western Species, New and Old — IV."

The Bryologist, March: — Best. "A Lesson in Systematic Bryology"; Fink, "How to Collect and Study Lichens"; Holzinger, "Some Recently Described North American Polytrichs"; Haynes, "Notes on a Colony of Hepatics found Associated on a Dead Fungus"; Crockett, "*Rhacomitrium heterostichum gracilescens*."

Bulletin of the Torrey Botanical Club, December: — Emerson, "Notes on the Blackening of *Baptisia tinctoria*"; Rydberg, "Studies

on the Rocky Mountain Flora — XIII"; Maxon, "A New Asplenium from Mexico."

Bulletin of the Torrey Botanical Club, January: — Livingston, "Chemical Stimulation of a Green Alga"; Arthur, "Amphispores of the Grass and Sedge Rusts"; Berry, "Additions to the Fossil Flora from Cliffwood, N. J."

Bulletin of the Torrey Botanical Club, February: — Spalding, E. S., "Mechanical Adjustment of the Suaharo (*Cereus giganteus*) to Varying Quantities of Stored Water"; Horne, "A New Species of Lembosia"; Maxon, "On the Names of three Jamaican Species of Polypodium"; Peck, "New Species of Fungi"; Murrill, "The Polyporaceæ of North America — X"; Harper, "Further Observations on Taxodium."

The Fern Bulletin, January: — Harper, "The Fern Flora of Georgia"; Davenport, "A New Type of Aneimia"; Hill, "*Equisetum scirpoides* in Illinois"; Van Hook, "Illinois Ferns near Lake Michigan."

Journal of Mycology, January: — Morgan, "*Sphæria calva*"; Seaver, "A New Species of Sphærosoma"; Arthur, "Sydow's Monographia Uredinarum, with Notes upon American Species"; Memminger, "*Agaricus amygdalinus*"; Kellerman and Ricker, "New Genera of Fungi published since the year 1900 [My. to X., with index]"; Kellerman, "Uredineous Infection Experiments in 1904"; Kellerman, "Elementary Mycology (continued)"; Kellerman, "Ohio Fungi, Fascicle X. List of Species and Hosts."

Journal of the New York Botanical Garden, January: — Nash, "Botanical Exploration of the Inagua Islands, Bahamas."

Journal of the New York Botanical Garden, February: — MacDougal, "Studies in Organic Evolution."

Journal of the New York Botanical Garden, March: — Hollick, "A Recent Discovery of Amber on Staten Island"; Nash, "The Flowering of *Nolina texana*."

The Ohio Naturalist, January: — Schaffner, "The Life Cycle of a Heterosporous Pteridophyte"; Gleason, "Notes from the Ohio State Herbarium — II"; Schaffner, "Mat Plants"; Schaffner, "Plants with Nodding Tips"; Riddle, "Brush Lake Algæ"; Scholl, "Key to the Ohio Hickories in the Winter Condition"; Cotton, "Key to Ohio Ashes in the Winter Condition"; Schaffner, "Key to Ohio Poplars in the Winter Condition."

The Ohio Naturalist, February: — Schaffner, "Key to the Genera of Ohio Woody Plants in the Winter Condition"; York, "The Hibernacula of Ohio Water Plants"; Schaffner, M., "Key to the Ohio Sumacs in the Winter Condition."

The Ohio Naturalist, March: — Wacker, "Ecological Notes on Ohio Pteridophytes"; Flory, "Key to the Ohio Maples in the Winter Condition"; Schaffner, "The Classification of Plants — I"; Schaffner, "*Lycopodium porophilum* in Ohio"; Schaffner, "The Struggle for Life on a certain Sandbar"; Riddle, "Notes on the Morphology of Philotria"; Tillman, "Ohio Plants with Tendrils"; Schaffner, "Key to Ohio Walnuts Based on Twig Characters."

The Plant World, December: — Safford, "Extracts from the Notebook of a Naturalist on the Island of Guam — XXV"; Blanchard, "Millspaugh's Blackberry."

The Plant World, January: — Bayley Balfour, "Physiological Drought in Relation to Gardening"; Brackett, "A Summer in the Tropics"; Watterson, "An Unusual Begonia"; Mansfield, "A Curious White Oak."

The Plant World, February: — Underwood, "A Glimpse at Early Botanical Literature"; Brackett, "A Summer in the Tropics (conclusion)"; Pammel, "Notes on some Plants of Northeastern Iowa"; Schneck, "Fasciation in the Cherry"; G[ager], "The Protection of Winter Buds."

Torreya, January: — MacDougal, "Discontinuous Variation and the Origin of Species"; Nash, "A Paspalum New to the West Indies"; Vail, "*Onagra grandiflora*, a Species to be included in the North American Flora"; Britton, "*Carex Underwoodii*, sp. nov."; Clendennin, "Twin Pine Embryos."

Torreya, February: — Shull, "Galtonian Regression in the 'Pure Line'"; Spalding, V. M., "Soil Water in Relation to Transpiration"; Murrill, "A Key to the Stipitate Polyporaceæ of Temperate North America — I"; Berry, "A Palm from the Mid-Cretaceous"; Britton, "*Galactia Curtissii* sp. nov."; Sumstine, "*Panæolus acidus* sp. nov."

Torreya, March: — Underwood, "The Early Writers on Ferns and their Collections — IV"; Clendenin, "Other Freaks of Peas"; Murrill, "A Key to the Stipitate Polyporaceæ of Temperate North America — II"; Britton, "*Jacquinia Curtissii* sp. nov."; Cockerell, "New Binomials in an Index."

Rhodora, January: — Brainerd, "Notes on New England Violets — II"; Fernald, "A Peculiar Variety of *Drosera rotundifolia*"; Dewey, "Identity of Prickly Lettuce"; Fernald, "*Ledum palustre* var. *dilatatum* on Mt. Katahdin"; Parlin, "Further Notes on *Arabis lævigata* and *Asplenium Trichomanes* in Maine"; Leavitt, "On Translocation of Characters in Plants"; Bartlett, "*Arenaria macrophylla* in Connecticut"; Robinson, "A Connecticut Station for *Lycopodium Selago*."

Rhodora, February: — Leavitt, "On Translocation of Characters in Plants (continued)"; Fernald, "A New Arabis from Rimouski County, Quebec"; Churchill, "Preliminary Lists of New England Plants — XVII"; Clark, "White Form of *Sabbatia chloroides*"; Beattie, "Remarks on Rhode Island Plants."

Rhodora, March: — Ganong, "On Balls of Vegetable Matter from Sandy Shores"; Fernald, "An Undescribed Northern Comandra"; Hall, "Vegetative Reproduction of *Spiranthes cernua*"; Bartlett, "A New Juncus of the Group Poiophylli"; Evans, "Notes on New England Hepaticæ — III"; and Robinson, "A well marked Species of Sparganium."

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